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The biogeography and conservation status of the rocky plateaus of the northern Western Ghats, India.

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THE BIOGEOGRAPHY AND CONSERVATION STATUS OF THE ROCKY PLATEAUS OF THE NORTHERN WESTERN GHATS, INDIA

By

Christopher John Thorpe

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Presentations and Conferences Attended:

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- 2012. March-April. Preliminary visit to the study area establishing contacts with Aparna Watve, the Maharashtra State Biodiversity Board office in Pune, Maharashtra, India and visiting potential survey sites.
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_____

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Abstract

Christopher John Thorpe

The biogeography and conservation status of the rocky plateaus of the northern Western Ghats, India

Rocky plateaus are globally threatened ecosystems and the lateritic plateaus in northern section of the Indian Western Ghats/Sri Lanka Biodiversity Hotspot (NWG) are notable landscape features. The NWG are geologically distinct from and biologically isolated from the other two sections of the Western Ghats. The NWG is known to possess elevated levels of endemic flora their biotic relationships remain poorly understood. We present here the first quantitative multi-taxa comparative study of plateau fauna in the northern Western Ghats. Ants, water beetles and amphibians were selected for the comparison as they use different ecological resources from each other and at various times of year therefore may provide a wider representation of plateau usage. Distribution and endemism were expected to reflect distribution and isolation by plateau and inter-plateau environment related to elevational, latitudinal, climatic and land-use clines. The study explored patterns of amphibian, water beetle, ant and fungal distribution and sampling seasonal pools and terrestrial surfaces of 13 representative plateaus in western Maharashtra, with sites ranging from 67-1179 m and across 2° of (sub) tropical latitude. Distribution of all taxonomic groups was spatially non-random at all levels of organisation and across all spatial scales. At the macroscale assemblages differed significantly with climate related to elevation, latitude but at a local scale land-use and microhabitat availably had an impact. Ants displayed a large seasonal assemblage variation, responding to seed availability. Water beetles the ants (combined survey data) were the best surrogates for all taxa data with amphibians the weakest representatives. Infection by the fungal pathogen, *Batrachochytrium dendrobatidis,* was extensive but less intense below the escarpment. We report the first records of

infection in 13 endangered and data deficient amphibian species in the Western Ghats. The plateaus of western Maharashtra have recently been recognised as fragile and threatened ecosystems most still lack adequate statutory protection. In the absence of peer reviewed comparative data, the importance of individual sites is difficult to demonstrate hampering evidence-based conservation decisions.

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Chapter 1. Introduction

1.1 Origin of the study and the research premise

The study that is the basis of this thesis had its genesis in 2008 when on a monsoon field trip to India a team from the British Herpetological Society visiting a rocky lateritic plateau in the hills of Western Ghats-Sri Lanka Biodiversity Hotspot (WG; Chorla Ghat, 15.6650N, 74.1379E; Fig 1.0-1 [Myers et al. 2000; Sloan et al. 2014; Lewis et al. 2010]). Diverse amphibians were observed using the shallow temporary pool systems and loose rocks for egg deposition, mate attraction and refugia. As any break in the rains would lead to rapid pool drying and their larvae dying. The behaviour seemed a high-risk strategy when there were more stable resources accessible, for example, a stream and paddy fields within half a kilometre. On returning to the UK a study was proposed to investigate why and how amphibians used these unusual and apparently high risk habitats. That concept has developed into the comparative study of the scattered rocky plateaus in the northern section of the WG that is the basis of this thesis.

The thesis is presented as an introduction followed by six research chapters drafted as complementary scientific papers, two of which are already in press, and concluding with a discussion after the final research chapter.

The northern Western Ghats (NWG) are geologically distinct and biologically isolated from the rest of the WG. The NWG are characterised by rocky plateaus (plateaus) formed from a secondary material, ferricrete of laterite, the plateaus are of high ecological contrast to the surrounding countryside. They are patchily distributed and found as hilltop carapaces above the WG escarpment and large open areas below it (Fig 1.0-2). The plateaus of NWG may offer a model system as they offer relatively simple ecological system compared to the surrounding (sub) tropical forest. Their patchy distribution in space allows for tests across clines in elevation, latitude and rainfall at differing spatial scales. The working hypothesis that is explored in this thesis is that geological, climatic and

topographical elements combine to regulate dispersal between plateaus causing them to act as terrestrial islands. To test the hypothesis distribution and abundance of three ecologically different taxa were examined together with one obligate mutualist (a fungal pathogen). The study aims to answer the simple question 'how does biodiversity vary between individual rocky plateaus in the NWG?' and 'what drives the differences?' If there is variation 'does the pattern of each taxon's distribution reflect any or all of the others?'

1.2 The Western Ghats-Sri Lanka Biodiversity Hotspot

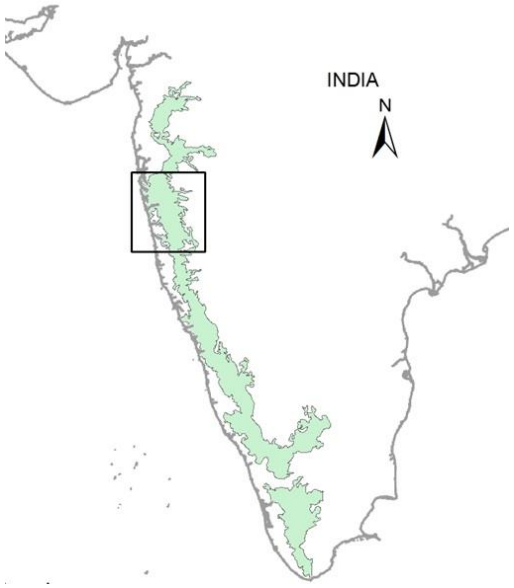

Figure 1.0-1 The location of the Western Ghats (green hatched) section of the Western Ghats-Sri Lanka Biodiversity Hotspot, India (Myers 2000). The study area is outlined in black.

The WG are a 1500km chain of hills trending north/south and parallel with the south west coast of India bounded on the west by an erosional escarpment (Fig 1.01). One of Conservation International's Biodiversity Hotspots and parts a UNESCO 2012 Natural Criteria World Heritage Site they are recognised as being of great biological and geographical significance (Myers et al. 2000; Brooks et al. 2006; Goyal et al. 2009; Mittermeier et al. 2011; IUCN 2012). The lateritic plateau at Kas was named

in the Sahyadri Group of the 2012 UNESCO listing; it is similar to the study plateaus above the WG escarpment. The WG are ranked among the top eight biodiversity hotpots and one of the three most threatened by human population growth (Cincotta, Wisnewski & Engelman, 2000; Sloan et al. 2014).

The IUCN Red List reports 39% of the WG species to be at risk of extinction (Gunawardene et al. 2007). With only 10% of the WG 'important but highly fragile ecosystems' afforded protected status, the risk of unique habitats being lost or damaged before their biology is understood sufficiently for conservation is high (Goyal et al. 2009; Bharucha, 2010; Kasturirangan et al. 2013).

1.3 Palaeontology of India and the study area

India and Sri Lanka were part of the super continent Gondwanaland which started to break up 158-160 million years ago (mya). Early in the break up India-Madagascar separated from what was to become East Africa (Briggs, 2003). Then around 130mya India-Madagascar parted from Antarctica followed by India-Seychelles separating from Madagascar between 84-96mya, triggered by the continent passing over the Marion hotspot (Briggs, 2003). Chatterjee et al. (1996) suggest the rifting may have been caused by a meteoric impact on the Indian western continental shelf. The resulting Shiva crater indicates a meteor of some 40 km diameter and maybe contiguous with the Chicxulub impact in the Yucatan. Traditionally it was thought India and Sri Lanka rifted away from the Seychelles bank 65mya carrying with it a flora and fauna of old world species and remained isolated from other landmasses as its' plate drifted north in the Indian Ocean towards Eurasia (Briggs, 1995). Briggs (2003) suggests it was around this period (55.5 -66mya) that the first contact between India and Eurasia took place, although it was another 6.5 million years before the entire northern margin of India fused. Lamb et al. (1998) concur putting the first contact at 55mya but Lunine (1999) place it at only 40mya.

At the end of the Cretaceous, ~65mya, as the Indian Plate moved north passing over the Réunion hotspot a massive series of volcanic eruptions, lasting around a million years, took place, disgorging ~1,000,000 km^3 of basalt (Widdowson & Cox, 1996). The lava formed the Deccan Traps (DT) Continental Food Basalt (CFB; 17°–24°N, 73°–74°E). Today the DT covers between 500,000 km2 (Widdowson & Cox, 1996) and 200,000 km2 (Lunine, 1999) of southwest India, in part under the Indian Ocean. The basalt is up to 3000 m thick in the west tapering to <100m in the east (Sonkamble et al. 2012). The western margin of the terrestrial basalt forms the range of hills known as the Western Ghats (Widdowson &Cox, 1996). At the western or seaward edge, of the DT the basalt has weathered to form an erosional escarpment. Kale et al. (2008) did not find any geomorphological evidence to explain the creation of the escarpment by tectonic mechanisms. The escarpment edge has retreated eastwards from its original offshore location to its present position ~30 km inland (Widdowson & Cox, 1996). The erosional forces on multiple layers of basalt have created the stepped hills we see today that give the Deccan Traps its name, derived from the Scandinavian 'trappa' meaning stairs. Below the escarpment the topography has slight variation (0-~200 m above sea level [m]), with low hills with a slight fall north to south and forms an area known as the Konkan (Widdowson & Cox, 1996). Above the escarpment the WG topography is highly heterogeneous with a slight fall north to south similar to that of the Konkan.

Modern revision of the palaeontology indicates that it retained enough connectivity with other landmasses to exchange species up to the end of the Cretaceous (Prasad et al. 1986; Prasad et al. 1988; Kar et al. 1986; Briggs, 2003). Whatley et al. (2000) found that endemic Ostracoda, a group that are found on some of the study sites, have Asian, African and European relationships and date from the upper Cretaceous. Briggs (2003) states that India lacks evidence of novel species that would have been expected to evolve in a 30-million-year period of isolation. A statement that is challenged as evidence of speciation is published for example (Van Bocxlaer et al. 2009; Li et al. 2013; Toussaint et al. 2017).

1.4 Study area geology and ferricrete hydrology

Over the last ~65 million years the NWG basalt has modified as a result of intensive in situ chemical weathering under tropical temperatures and high rainfall into ferralitic soils and laterite (Widdowson & Cox, 1996; Goudie, 1973). Within these soils all the primary materials have been decomposed or leached leaving quartz, neo formed kaolinite with iron and aluminium secondary oxides (Goudie, 1973). Aluminium, iron or calcium can be the dominant metals in laterite but in the northern Western Ghats (NWG) ferruginous laterite is the dominant form in the NWG (Devaraju et al. 1993). The chemical composition of laterite varies above and below the escarpment (Widdowson & Cox, 1996).

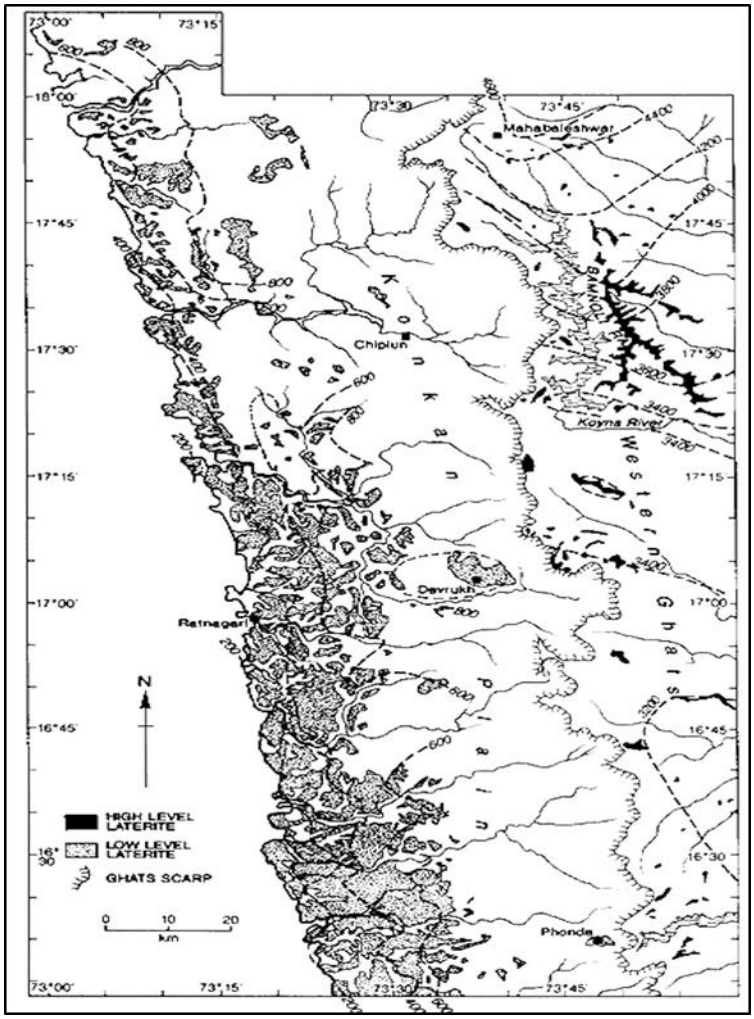

Figure 1.0-2 Laterite is patchily distributed. It forms hilltop carapaces above the Western Ghats escarpment and open plateaus below in the Konkan. The laterite is chemically different either side of the escarpment. The map illustrates most of the study area, with only a small area to the south not shown. Reproduction is by kind permission of Mike Widdowson.

The study plateaus are ferricretes of laterite which are self-stabilising duricrust formed when the laterite is exposed to the air and occur as hilltop carapaces above the WG escarpment and open expanses below it (Fig 1.0-3). Occurring between 15°60' and 18°20'N and from the west coast to 74°E and up to 1200 m (Goudie, 1973: Widdowson & Cox, 1996). These plateaus are known in Mahrati as 'sadas'. Widdowson & Cox (1996) report the laterite originally formed a blanket over the parent material which was subsequently eroded through to produce the current landscape. The blanket view is challenged with the suggestion that the carapace ferricretes originated as valley bottom laterites and through a process of landscape inversion have arrived at their present position (Ollier et al. 2008). The shape of the current carapaces in many cases supports the valley bottom hypothesis Ollier et al. (2008) site the ferricretes around Mahabaleshwar and others which have long linear shapes.

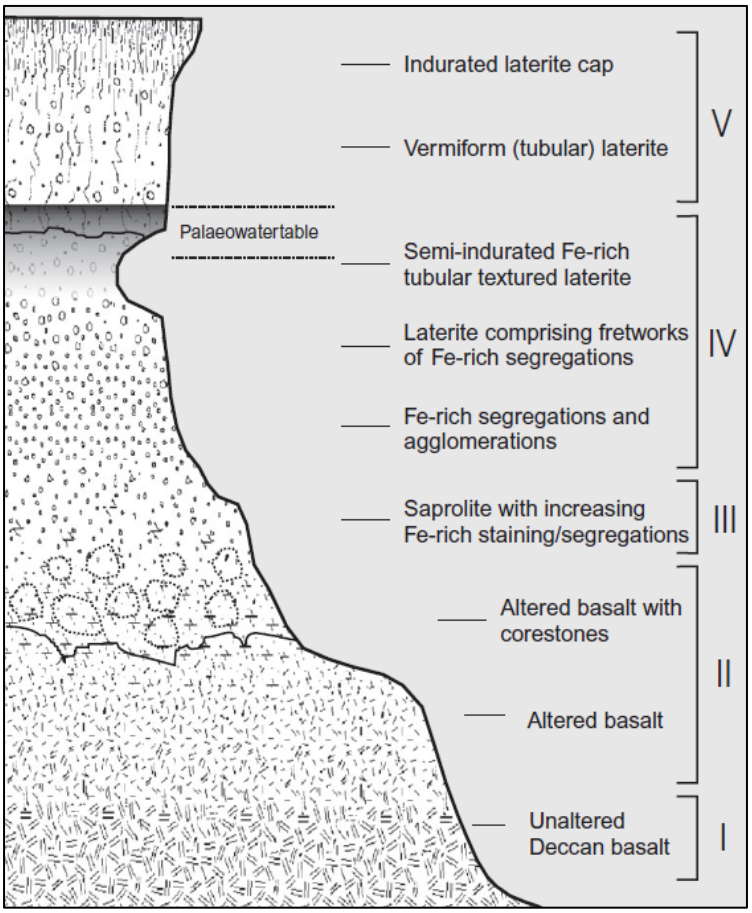

Figure 1.0-3. A typical cross section of laterite as seen in the study area demonstrating its stratified construction and porous character. Reproduced by kind permission of Mike Widdowson.

The lateritic soils above the escarpment have a very low pH 4.5-5.9 and are characterised as acidic oxisols (Dikshit, 2002; Watve, 2010; Watve, 2013) plateau soils have been found to range from sandy to sandy loam and are rich in organic carbon, available nitrogen and potassium but depleted in phosphorus (Watve, 2010; Watve, 2013).

The hydrology of the plateaus is poorly understood but Goudie (1973) reports that Maharashtra laterite is more porous than samples from sites in Ireland and Botswana with an absorption value of 9.6% (Fig 1.0-3). Even with this level of porosity most of the water runs off them rapidly in the monsoon rains leading to spate conditions in all proximate water courses with temporary flooding of any depressed areas on the plateaus. The fractured physical nature of the laterite may provide refuge sites for some taxa (Fig 1.0-3).

Beyond the northern extent of the distribution of lateritic plateaus there are basalt plateaus or outcrops occurring 18°20'-21°N and 73°35'-73°50E with elevations of 900-1100 m (Watve, 2013; Jog et al 2002). They have similar appearance to the ferricretes in that they have little vegetative cover and are broadly level but they occur as plains between hills rather than hill top carapaces.

1.5 Inselberg comparison

Until the early 2000's very little ecological research had taken place on the rocky plateaus of the northern Western Ghats and even now few papers have been published. In the early 2000's Stephan Porembski, an expert in inselberg ecology, became interested in the plateaus and with my co-supervisor, Aparna Watve, published comparison of their ecology with that of inselbergs (Porembski & Watve, 2005). Inselbergs having been studied for longer may provide a useful comparative model.

Inselbergs, both granitic or gneissic, and the lateritic plateaus share similar environments which may have made them edaphic islands in sea of contrasting matrix (Porembski & Watve, 2005). Michael et al. (2010) describe inselbergs as a 'naturally heterogeneous and spatially-limited habitat' adding to the regional habitat heterogeneity. In addition to isolation from a contrasting matrix temperature clines resulting from elevational may regulate environmental suitability and produce a dispersal barriers. Tropical species are acclimatised to narrow thermal bands with dispersal and distribution restricted by temperature (Janzen, 1967; Ghalambour et al. 2006; McCain & Sanders, 2010).

At a macro-scale inselbergs and rocky plateaus appear to have a single environment but as Michael et al. (2010) stated inselbergs are naturally heterogeneous:

- Thin or no soil cover.
- Low nutrient availability.
- Elevated temperatures.
- Large diurnal to nocturnal temperature changes.
- Xeric conditions.
- Limited vegetation.
- Highly specialised vegetative forms; Ephemeral flush vegetation, monocotyledonous mats (Porembski, 2007).
- Nutrients accumulate downslope leading resulting in a different floral assemblage (Porembski, 2000).

That basic description has now been applied to lateritic plateaus. Within-site they are found to be made up of a mosaic of micro habitats like those of inselbergs (Porembski et al. 2005; Porembski, 2007; Watve, 2013):

- Exposed rock where it forms large areas on the plateaus can be considered a ‘micro-environmental desert (Porembski et al. 2005).
- Environmental extremes, seasonal changes from xeric to hydrophilic. Large diurnal to nocturnal temperature variation (Watve, 2010, 2013)
- Loose rocks provide refugia for both reptiles and invertebrates (Goldsbrough et al. 2003).
- Both exposed rock and loose rock have a cryptogamic crust comprising a covering of cyanobacterial crust together with communities of lichens both foliose and crustose.
- Where rock or boulder surfaces have been broken down to provide a foothold, lower plants are found including both mosses and ferns.
- Rock crevices provide a micro environment for plants and refugia for reptiles which show specialist adaptations (Michael et al. 2010).
- Soil filled depressions, sometimes large and often the only habitat for woody plant species. The lack of soil on inselbergs is a factor limiting floral succession to forest species (Sarthou et al. 2010).
- Shallow water pools, tending to be exclusively vernal with longevity of a few days to a few months. On the plateaus they have a depth of 25 to 100mm. They have their own floral and faunal communities.
- Deeper pools with water 100mm to 500mm. Formed in depressions they often have associated accumulated soil. On the plateaus they have similar communities to the shallow pools with the addition of floating hydrophytes (Watve, 2013).
- Semi-permanent water. Deeper pools on plateaus, often man made, with a depth exceeding 500mm. On plateaus they have a hydrophytic plant community and a complex invertebrate assemblage.

- Drainage channels form over time and provide a different habitat to pools with flowing water during the rains. The deeper channels on the plateaus display a unique flora on the channel walls (Watve, 2013).

- Inselberg plant communities are often comprised of specialised species with elevated levels of adaptive traits often annuals and frequently with life history strategies to accommodate low nutrient status. With elevated levels of endemism (Watve, 2013). They tend to flower at the same time giving rise to term Ephemeral Flush Vegetation (EFV) a term originally coned by Richards (1957) and applied to the plateaus vegetation for the first time by Porembski et al. (2005).

- Porembski et al. (2000) found soil particles and nutrients accumulate at the base of slopes especially where water flow is impeded by vegetation or topography.

1.6 Northern Western Ghats environmental drivers of biotic distribution

The study area extends over ~2° latitude (15.89°-17.92°N) and encompasses plates from almost sea level to 1179 m. Rainfall seasonality increases south to north in the study area with the northern plateaus experiencing ~11% fewer days of rain each year. Below the escarpment rainfall deposition is under 2000 mm (Hobbhahn et al. 2006) and averages 6000 mm above with its greatest volume along the escarpment ridge (Gadgil, 2004).

The complex topography above the Western Ghats escarpment has created multiple abiotic niches resulting from elevational and latitudinal clines in temperature, rainfall both amount and duration. In mountainous areas, especially in the tropics, this is known to produce discrete isolated populations with asymmetric gene flow (Janzen, 1967; Qian et al. 2014; Stein et al. 2014). The effect is not uniform but dependent upon taxonomic group, trophic level and the scale of observation (Qian &

Kissling, 2010; Binkenstein et al. 2017). Spatial grain and spatial extent of observation are key factors influencing the strength of the positive heterogeneity–richness relationship and should be considered in a study design (Stein et al. 2014). Speciation rates are higher in mountainous areas at the same time populations experience lower extinction levels (Hoorn, 2013). The process is reinforced over time with species located in areas of low topographical variation having to move relatively further to accommodate climatic change than those in areas with high relief. In the tropics the rate of change is a critical factor (Janzen, 1967; Ghalambor et al. 2006; Hoorn, 2013). Vicariant arthropods have been found to diverge rapidly, when isolated by orogeny, into groups when subjected to climatically different areas (Brower, 1994). The isolation and divergence can be at a fine scale leading to 'sky islands' with unique species on each even when near (Endo et al. 2015). An effect observed at genus and species in birds in the southern WG (Robin et al. 2010, 2012 & 2017). We would anticipate higher species richness in the 'mountainous' area above the escarpment relative to the lower relief habitat below the escarpment in the Konkan.

The study will not examine species distribution in the matrix but island biogeography theory may be useful in commenting on assemblages, especially if taxa are plateau specialists. Classical island biogeography would lead us to expect island size and remoteness from a source population to structure species assemblages, richness and endemism (Lomolino et al. 2010, pp. 534-590). As in Fig 1.0-2 laterite is very scattered above the escarpment except for a large areas in the north. Below the escarpment it occurs widely but becomes patchy to the north. The numbers of species is expected to be low and the number of endemic allospecies relatively high where colonisation rates are low (Lomolino et al. 2010, pp. 557). Anthropogenic activity can act in a non-random way causing extinctions or community disassembly (Lomolino et al. 2010, pp. 565). We may therefore expect undisturbed plateaus that are geographically isolated (for example Zenda and Amboli High) to have low number of species with a high number of endemics (Fig 1.0-4). In comparison a low disturbance site which is not isolated (for example Jagmin) would have more species and more non-endemic species (Fig 1.0-4). Sites that are close together should share more species for example Amboli Low

and High and all those in the north above the escarpment but particularly Chalkewadi and Jagmin (Fig 1.0-4).

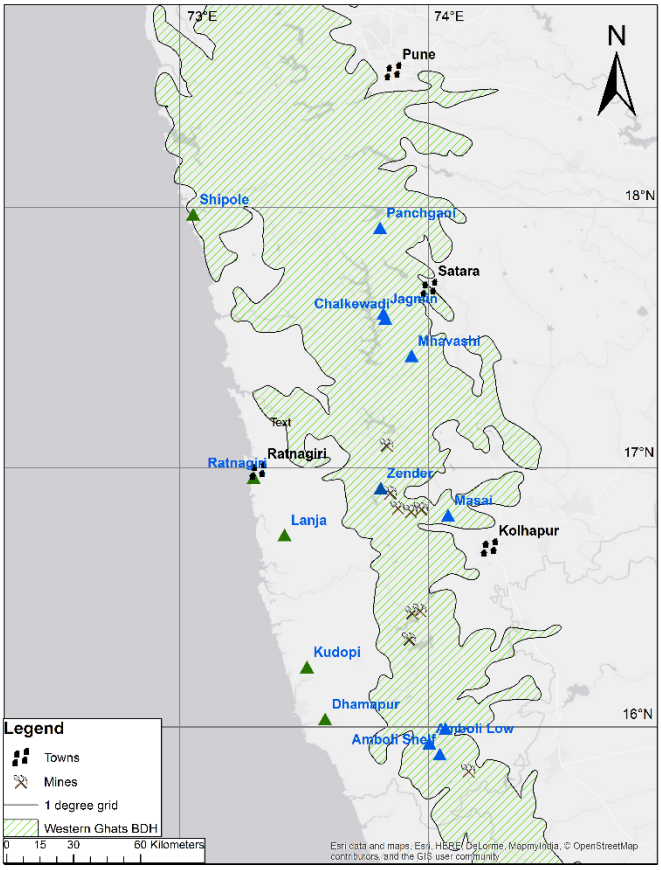

Figure 1.0-4. The location of study sites investigated from 2012 to 2014 with town locations included as reference points. Some mine sites are included to illustrate the area most threatened by open cast mining.

Plateau habitat suitability is determined by taxa specific abiotic factors summarised in Table 1.0-1. As In the NWG these may be acting both to provide suitable habitat but also to exclude taxa whose tolerances are exceeded. With inter-site elevational differences exceeding 1100 m, and the ~500 m step up escarpment, temperature may regulate both dispersal and distribution (Ghalambor et al. 2006). Plateau surface temperatures have been recorded at over 50°C (Watve, 2010; Watve, 2013). Such extremes may be avoided by behaviour or thermal plasticity (Bogert, 1949; Marais & Chown, 2008; Gunderson & Stillman, 2015). Temperatures over 28°C exceed the optimum for tropical terrestrial

ectotherm fitness (Deutsch et al. 2008); although specific tolerances are recorded up to ~54°C in Mediterranean water beetles (Arribas et al. 2012).

Amphibians have the lowest upper thermal tolerance of terrestrial ectotherms at a mean of 35.3°C (Pincebourde, 2016), for example *Rhacophorus malabaricus* in India die in pools above 34°C (Daniels, 1991). Amphibian behavioural avoidance often relies on suitable microhabitats and their distribution has been investigated in this study (Woods et al. 2015; Pincebourde, 2016).

In aquatic Coleoptera temperature is again an important regulator in distribution. Thermal tolerance has been linked to the ability to access adequate oxygen in tracheaeted arthropods and in turn limit their thermal tolerance as metabolic oxygen demand outstrips the bio-availability of dissolved oxygen (Verberk & Bilton, 2013). There are two mechanisms to explain the availability of oxygen to aquatic invertebrates, partial pressure which decreases with altitude and solubility which decreases with temperature, thus increasing with altitude. Solubility is reduced by solute presence in the water (Verberk et al. 2011). Oxygen availability declines by 80% from sea level to 4,000 m whereas mean weight-specific respiratory demand only decreases by 50% indicating a theoretical shortfall increasing with altitude (Jacobsen et al. 2003) An Oxygen Supply Index (OSI) proposed by (Verberk et al. 2011) suggests a solution incorporating both drivers. They conclude that in warmer environments the oxygen demand of an organism can exceed supply and larger organisms would be found at lower temperatures. Within a single temperature regime dissolved oxygen was found to be a good predictor of taxonomic richness in isolated pools (Starr et al. 2014).

Elements of water quality, other than temperature, have an impact on suitablity. Pool pH is likely to reflect edaphic conditions where soils are highly acidic, 4.5-6, (Dikshit, 2002; Watve, 2013). Macro-invertebrates are reported to be intolerant of pH values below 5.5 (Friday, 1987). pH is known to be important in the distribution of amphibians (Gururaja et al. 2013). Aluminium and iron are

concentrated in the plateau lateritic soils, their impact on biota in the study area is unknown (Goudie, 1973) but both $^{H+}$ and Al^{3+} have been shown to be detrimental to some freshwater invertebrates. Aluminium and the % concentration of Al^{3+} have higher concentrations in water with a pH < 5 (Gensemer et al. 1999) Al^{3+} is the dominant species at a pH value between 3.8-4.2 (Clark et al. 1985). Bioaccumulation of aluminium is influenced by pH in particular low pH (Wren et al. 1991). Macroinvertebrate species richness is known to decline rapidly in waters with an Al^{3+} concentration above 0.42mg/L and is known to be toxic to amphibians (Clark et al. 1985). Water pH is reported to be slightly higher (6.7-6.8) than soil values possibly because of pool flushing by heavy rainfall. Dytiscidae though display specific responses to pH with a broad range of tolerances therefore pH may be an ecological filter in these systems (Gioria, 2014).

In a study of two rivers in Spain Aluminium was found to be less important than other metallic ions to invertebrates (Ca, Fe, K, Mg, Na, Cu, Zn) but overall water conductivity was still an important structuring variable for aquatic Coleoptera (Benetti & Garrido, 2010) and is an important driver of water beetle assemblages (Picazo et al. 2012) also for amphibians whose occupancy increases with increasing conductivity (Klaver et al. 2013). The concentration of many water-soluble ions is correlated with water temperature and therefore conductivity, salinity, specific ion concentration and pH can be expected to covary with elevational related temperature (Valladares et al. 2002, Biggs et al. 2005). Macroinvertebrate β-diversity changes with electrical conductivity (Florencio et al. 2014). Conductivity increases with pool age, co-varying with hydroperiod which may be shorter below the escarpment and in the north of the study area (Valladares et al. 2002). Pollution negatively impacts aquatic Coleoptera depressing species richness, abundance and diversity (Benetti et al. 2010).

Water availability in the NWG varies dramatically through the year as the area is monsoonal but also by elevation. The arrival of the rain transforms a very dry plateau surface to a seasonal wetland with many pools. Taxa within such a system are behaviourally adapted to survive the dry season with plants surviving as seeds and completing their life cycle in the rains as in the ephemeral flush

vegetation (Porembski & Watve, 2005) or withdrawing resources into the core as in resurrection plants (Hopper, 2000). The length of the hydroperiod is important for amphibians (Babbitt et al. 2003) and water beetles (Tarr et al. 2005). Both show seasonal assemblage changes during the wet period. Explosive breeding amphibians appear as soon as the rain starts with some leaving as soon as reproduction is finished (Chan, 2003; Gaitonde et al. 2016). Water beetle assemblages are dominated by early colonising predatory Dytiscidae in new pools (Fairchild et al. 2000). As pools dry the assemblages change to communities of species able to tolerate poor water quality where solutes concentrate (Florencio et al. 2016). The only other NWG plateau ant studies (unpublished) found ant communities to be seasonal (Fernandez, 2013, Baidya, 2015) with Baidya's (2015) study linking the change to seed resource availability. They both found plateau ant abundance and richness to be negatively impacted by the monsoon.

Site occupancy in two of the focal taxa may be impacted by predation. Water beetles are cannibalistic and predated upon by other fauna including amphibians (Sen-Her & Yao-Sheng, 2010; Gioria, 2014). Fish are predators of macroinvertebrates and amphibians in all their life history stages (Arnott, 2006, Scheffer et al. 2006). Their presence changes species assemblages and reduces pool beetle biomass by 66% (Fairchild et al. 2000). Coleopteran dispersal to predator free pools (fish and Odonata) is known in the tropics (Larson, 1997). As predators are biotic entities in their own right they are subject to the same environmental constraints as their prey frequently resulting in covariance (Gioria, 2014). However, they may be more susceptible to small shifts in pool hydroperiod (Eyre et al. 1992; Jeffries, 1994; Gioria, 2014). Vernal pools, especially very temporary pools, may offer predator free space to study taxa.

Table 1.0-1 Summary of the known abiotic drivers of distribution for the focal biota.

Taxa	Abiotic Factor	Impacts	Author
Amphibians	Hydroperiod	Species richness increases with length of hydroperiod	Babbitt et al. 2003

	Start of rains	Triggers breeding	Chan 2003, Gaitonde et al. 2016
	Conductivity	Occupation increases with conductivity	Klaver et al. 2013
	pH	Regulates species presence	Gururaja et al. 2013
	Temperature	Maximum of 35.3°C	Pincebourde et al. 2016
	Microhabitats	Avoidance of high temperatures	Woods et al. 2015
Aquatic Coleoptera	Start of rains	Early Dytiscidae dominance	Fairchild et al. 2000
	Hydroperiod	Genera and abundance increased with longer hydroperiod	Tarr et al. 2005
	Pool drying	Community shift on drying	Florencio et al. 2016
	Water conductivity	Lower species richness, abundance and diversity	Benetti et al. 2010
	Water conductivity	β-diversity changes	Florencio et al. 2014
	pH	Lower numbers pH<5.5	Friday 1987
	pH	Species specific response filters occupancy	Gensemer et al. 1999; Gioria 2014
	Al^{3+}	Linked to low pH toxic to some species.	Gensemer et al. 1999; Wren et al. 1991
	O_2	Taxonomic richness	Starr et al. 2014
Ants	Seed availability (seasonality)	Dominance of functional groups	Baidya 2015
	Temperature	>28°C exceeds thermal tolerance of some species	Deutsch et al. 2008
	Rainfall	Depresses ant activity	Baidya 2015; Fernandez 2013

Plateau biota may be reliant on the variable mosaic of microhabitats. They bear many similarities with inselberg habitats which have received greater research; both are included but filtered for applicability to the focal taxa (Porembski, 2000; Watve, 2013).

- Exposed rock surfaces. Always covered in a biological film or cryotogamic crust comprised of cyanobacteria, crustose lichens and green algae. Important in nutrient cycling and soil formation which supports small ephemeral plants. Easily damaged by anthropogenic activity.
- Loose and buried rocks. These provide refugia for many taxa and may have a thermoregulatory role for some. They provide amphibian calling perches and display sites for some reptiles (Gaitonde et al. 2016).
- Rock crevices. May have a role in thermoregulation and refugia in the dry season.
- Open. These are thought to provide refugia for many taxa.

- With vegetation. They hold moisture beyond the rains and have an associated flora. Larger crevices can hold woody plants.
- Depressions in the rock surface:
- Soil filled depressions. Have a flora dependent upon their depth. The deeper depressions hold woody plants.
- Pools in depressions. Vernal pools on rocky plateaus have their own adapted flora and fauna are known to have a key role in maintaining regional biodiversity (Jocque et al. 2010, Brendonck et al. 2015, Padhye, 2015; Padhye & Victor, 2015).
- Surface flooding. Not often considered as a microhabitat but is in effect a network extensive shallow, <50 mm, pools which are very temporary lasting only as long as it rains.
- Streams. Not often considered on rocky plateaus but they are formed for the duration of the monsoon where water runs off the site. Known to be important for some amphibians adapted for lotic systems or their associated habitats (Bhatta, 1998).

1.8 Current status of the biogeography of the northern Western Ghats

Biotic isolation is known at several scales and in a range of taxa in Peninsular India. The Western Ghats and Sri Lanka were originally thought of as biologically very close as they were part of the same plate when it broke away from the rest of Gondwana 135 million years ago (MYA). It is now known that, whilst there are faunal similarities between Sri Lanka and the Indian mainland, Sri Lanka has its own distinct fauna (Bossuyt et al. 2004). They showed that in two invertebrate and four vertebrate groups that faunal exchange between the two countries over the last 500,000 years has been limited. The fauna in India contain both Gondwanan relicts and species that migrated into India after its accretion with Eurasia between 55 MYA (Lamb, 1998) or 40 MYA (Lunine, 1999; Van Bocxlaer,

et al. 2006; Ali, 2008; Li et al. 2013; Barley, 2014; Toussaint et al. 2016) with vicariant taxa speciating in India (Dutta, et al. 2004; Biju, et al. 2009).

The WG are not a biological continuum but show restricted gene flow resulting in population genetic isolation dividing the WG into three biological regions summarised in Table 1.0-2. Around 10°N there is a break in the WG hills known as the Palghat Gap separating the southern from the central WG. There is limited gene flow across the gap for elephants (Vidya et al. 2005) and Lion-tailed Macaques (Ram et al. 2015). In birds, the White-bellied Short Wing, *Brachypteryx major* populations either side of the Palghat Gap are reported to have genetic distances between 8.9-9.2%, enough perhaps to differentiate them as separate species (Robin et al. 2010). Isolation exists between bird populations on hilltops; the southern and central WG resulting in separation at generic as well as species level (Robin et al. 2010; Robin et al. 2012; Robin et al. 2017). There is a smaller gap, the Goa Gap, between the central and northern WG. In an analogous way to the genetic isolation seen between central and southern WG bird populations and the endemic amphibian family Nyctibatrachidae demonstrate clade endemism (Van Bocxlaer et al. 2012). Their study identifies regional species clusters separated by the discontinuities in the WG, suggesting isolated populations under differential ecological pressures at a sub-regional scale. A result being more recently demonstrated in other amphibian genera, for example Ranixalidae (Dahanukar et al. 2016; Garg et al. 2016) and Fejervarya (Garg et al. 2017).

In the NWG the volcanic eruptions that created the Deccan Traps biologically sterilised the area. All taxa found in the study area have migrated in as the lava cooled and the erosional landscape developed which may have isolated some populations. The rocky plateaus that characterise the isolated NWG are described by Bharucha (2010) as ‘cryptic and specialised landscape elements’ which need preserving but he notes ‘there is an absence of locale specific data’. Threats include grazing, wind turbine installations, trampling from tourism, fire and mining (Joshi et al. 2004;

Kodandapani et al. 2004; Pande et al. 2013; Thorpe et al. 2016). Whilst the plateaus of western Maharashtra have recently been recognised as fragile and threatened ecosystems, first by the Western Ghats Ecology Expert Panel and subsequently by the central government Higher Level Working Group chaired by Dr K. Kasturirangan, most still lack adequate statutory protection (Bharucha, 2010; Kasturirangan et al. 2013).

In the absence of comparative data, the formation of evidence-based conservation policy is problematic (Adams et al. 2013; Rose, 2015; Sutherland et al. 2017). In addition to helping to inform conservation policy, this study will assist with two other data shortfalls: the Wallacean shortfall (Lomolino et al. 2010) and the Hutchinsonian shortfall (Hortal et al. 2015). With new species regularly being described from the NWG there is inevitably a lack of complete understanding of species distribution and range size i.e. the Wallacean shortfall. In addition, little is known about individual species abiotic tolerances regulating their distribution i.e Hutchinsonian shortfall. Hortal et al. (2015 pp. 525) have proposed a refinement to the definition of the Hutchinsonian shortfall suggesting 'the response and tolerance of species to their abiotic environment'. Whilst type localities for NWG species are known their ranges and the reasons for their distribution are poorly understood for example in their review of the amphibian genus *Philautus* Biju and Bossuyt (2009) describes several species only from museum specimens or a single location. Some limited information has been published for amphibian habitat associations for example Bhatta (1998) but none for aquatic Coleoptera or formicidae but see thesis by Fernandez (2013) and dissertation by Baidya (2015).

Table 1.0-2. Summary of macroscale patterns in biotic distributions at a range of spatial scales in the Western Ghats-Sri Lanka Biodiversity Hotspot.

Taxa	**Geographical scale of isolation**	**Author**
Amphibians (Philautus and Ichthyophis), freshwater fish, shrimps and crabs	Sri Lanka and mainland India	Bossuyt et al. 2004
Elephants	South and Central WG	Vidya et al. 2005
Lion Tailed Macaques	South and Central WG	Ram et al. 2015
Birds	South and Central WG	Robin et al. 2010 Robin et al. 2017

Birds	Central and North WG	Van Bocxlaer et al. 2012
Birds	Between hilltops South and Central WG	Robin et al. 2010, Robin et al. 2012
Amphibians (Nyctibatrachidae)	Sri Lanka-mainland India and South-Central WG, Central-North WG	Van Bocxlaer et al. 2012
Amphibians (Xanthophryne toads)	Within NWG, inter-plateau	Biju et al. 2009
Reptiles	Between plateau and matrix NWG	Chikane et al. 2012
Ants	Between plateau and matrix NWG	Fernandez 2013

Prior to 2005, when Porembski and Watve published their paper on ephemeral flush vegetation of the rocky plateaus in western Maharashtra, India, scant attention had been paid to these important landscape elements (Porembski & Watve, 2005). In the intervening years research has accelerated but almost exclusively in taxonomy e.g. Biju et al. 2009; Lekhak, 2012; Padhye, 2013; Kulkarni, 2014; Pandit, 2014; Padhye et al. 2015) but see also the thesis of Fernandez (2013) and dissertation by Baidya (2015) for information on ants. In common with most of these studies, the work on the chytrid pathogen *Batrachochytrium dendrobatidis* (*Bd*) substantially ignored the coastal area between the sea and the hills of the Western Ghats (Nair et al. 2011; Dahanukar et al. 2013; Molur et al. 2015).

Evidence of plateau isolation comes from reptiles, amphibians and plants, none offer a comparative plateau study. One of the few studies to investigate vertebrates on and around an NWG plateau found reptile assemblages on the plateau were different to those in the surrounding forest (Chikane et al. 2012). The amphibian regional species clusters are frequently comprised of plateau populations which may be isolated (Dahanukar et al. 2016; Garg, 2016). Novel amphibian genera and species are being described in the NWG from the lateritic plateaus; one *Xanthophryne tigerina* is only known from a cluster of plateaus less than 100 km^2 and *Raorochestes ghatei* from a small cluster of plateaus (Biju, et al. 2009, Padhye, 2013). In plants 58% of endemic species are found only on plateaus and some of those are only known from their type locality (Lekhak, 2012). Some of the streams flowing from the higher plateaus contain a unique freshwater genus of littorinid snails, *Cremnoconchus* (Reid et al. 2013) and species of fish restricted to single headwaters (Dahanukar et al. 2004; Dahanukar et al. 2012; Kharat et al. 2012).

1.9 Anthropogenic land uses in the northern Western Ghats

Traditional societies have used natural resources in the WG for ~3000 years and there has been organised state forestry for some 200 years (Chandran, 1997). More recently the NWG have come under increasing pressure from human population growth which places demands on the landscape including the rocky plateaus in western Maharashtra. Those directly related to the plateaus include:

- Microhabitat disturbance. Loose rocks are frequently collected from accessible plateaus for a range of human uses. Fodder and firewood are also collected. Some plateaus are burnt to encourage a beneficial change in flora. It is possible that some taxa on the plateaus are fire adapted (Kodandapani et al. 2004).
- Installation of wind turbines. The plateaus are generally quite level and have little overburden of soil making them ideal sites for wind farms. Internationally wind farms are known to change faunal assemblages (Cochran, 2013; Millidine et al. 2015) and cause increased bird mortality in the NWG.
- Mass tourism. Many plateaus have elevated locations with escarpment edges offering good views; they are cool and towards the end of the monsoon mass flowering of many plants. As a result, some of the road accessible sites attract large visitor numbers who collect flowers, trample vegetation and deposit refuse. The impact of this on the World Heritage site, Kas Plateau, is under investigation (Agarwal Personal Correspondence).
- Bauxite mining. Part of the laterisation process concentrates immobile metallic ions in the soil, iron and aluminium. With easy access and no overburden some plateaus make good mining prospects. The method is open cast which removes the complete ecosystem. So far it has proven impossible to adequately recreate a duricrust (Thorpe & Watve, 2016) and bauxite mining in the WG has been deemed unsustainably (Phillips, 2012).
- In addition, we must consider pool and site drying as a major disturbance type as it leads to the extinction of all taxa especially Coleoptera not in diapause (Svensson, 1985).

1.9.1 Research design

The thesis presents the outcomes of a study designed to find biotic realtionships between the NWG rocky plateaus, it is novel in several ways:

- It is the first comparative study of the biota of the lateritic plateaus in the northern Western Ghats.
- It is unusual in (sub) tropical studies as it incorporates terrestrial, semi-terrestrial and aquatic environments.
- Included in the biota is the fungal pathogen *Batrachochytrium dendrobatidis (Bd).*
- The study is also novel in its geographic extent by including plateaus from the area between the hills of the Western Ghats and the coast.

By selecting taxa which use different resources across space and time with varying dispersal abilities and then seeking concordant patterns between them the study hopes to be able to draw robust conclusions.

Ants (Formicidae) were selected as dry season specialists, aquatic Coleoptera chosen as obligate aquatic taxa and amphibians as many are semi-terrestrial in the NWG.

The study was designed to capture the differences in taxa distributions within the majority of the spatial extent of lateritic duricrusts in the NWG in order to have the best chance of capturing assemblage changes related to latitude and elevation (Fig 1.0-2).

Table 1.0-3 Site descriptions with latitude and longitude, elevation (m), land-use and Eco-zone.

Plateau	Latitude	Longitude	Elevation	Land use	Eco-zone
Chalkewadi	17.5736	73.8261	1157	Wind turbine	High North

Jagmin	17.5927	73.8181	1179	Light	High North
Mhavashi	17.4310	73.9313	1090	Wind turbine	High North
Panchgani	17.9217	73.8045	1131	Tourism	High North
Masai	16.8181	74.0779	974	Tourism	High Central
Zenda	16.9226	73.8072	1015	Light	High Central
Amboli Low	15.9374	74.0027	809	Tourism	High South
Amboli High	15.8903	74.0403	854	Light	High South
Shipole	17.9735	73.0527	170	Agriculture	Low North
Ratnagiri	16.9627	73.2962	67	Agriculture	Low Central
Lanja	16.7419	73.4204	156	Light	Low Central
Kudopi	16.2327	73.5105	90	Light	Low South
Dhamapur	16.0315	73.584	85	Agriculture	Low South

1.9.1.1 Study area

The study area (see Fig 1.0-2, 1.0-4) includes the selected 13 plateaus situated both above and below the North-South trending escarpment in the northern part of the 1600 km Indian section of the Western Ghats/Sri Lanka Biodiversity Hotspot. The number of plateaus in the study area is not known; whilst the distribution of laterite has been mapped the factors creating ecological dispersal barriers are poorly understood (Widdowson & Cox, 1996). The plateaus support a wide range of microhabitats, including a variety of water bodies from seeps to deep pools, all subject to seasonal drying (Watve, 2010; IMD, 2016; Thorpe et al. 2016). Rock pools are rare in the surrounding countryside which has porous topsoil. NWG plateaus are under pressure from several proximate anthropogenic threats: localised activities such as illegal hunting, extraction of non-timber forest products, livestock grazing, and fires, and landscape-level threats such as mining, road construction, hydro power projects, wind farms, large-scale agricultural expansion, creation of monoculture plantations, tourism and open cast bauxite mining (Cincotta, Wisnewski & Engelman,. 2000; Phillips 2012; Lad 2013; Balaji et al. 2014; CEPF 2016).

1.9.1.2 Sampling design and methodology

The sampling design was informed by exploratory investigations in 2012 which identified the variable nature of microhabitats and pools within individual plateaus and the distribution of accessible plateaus in the study area. Where possible study sites were paired plateaus one with marked anthropogenic disturbance and a companion with light disturbance (Fig 1.0-4survey; Table 1.0-3). Surveyed plateaus ranged from 67-1179 m ASL and occurred covering more than 2° of latitude (15.89-17.92 °N) (Fig 1.0-4; Table 1.0-3). To aid spatial analysis, the study area was divided into 2 Regions by the escarpment (above the escarpment >700 m ASL and below the escarpment < 700 m ASL) with each of these arbitrarily sub-divided into 3 latitudinal sections (North, Central and South) creating six notional eco-zones (Fig 1.0-4; Table 1.0-3). To assess spatial variation the 13 representative plateaus were selected, covering most of the latitudinal distribution of basaltic laterite in the NWG (Fig 1.0-2, 1.0-4). In each year (2013 and 2014) All 13 plateaus were visited, on each occasion:

- Six pools were selected, for water beetle sampling, on each plateau visited, encompassing the range of pool types present on each occasion.
- Four belt transects of 100 m x 6 m were set out, for amphibian sampling, to encompass all the microhabitats present.
- In the dry season two ant surveys were conducted on the same plateaus. On each occasion 4 survey lines were established to encompass all the microhabitats present and along each 10 sweet baited traps were placed to be collected 24 hours later.

The same 13 plateaus were sampled in both 2013 and 2014. Pools, transects and survey lines sampled on individual plateaus differed between sampling occasions. To minimize inter-year variation in assemblage structure, pools on the same plateaus were sampled in the same calendar weeks each year.

1.9.1.3 Research objectives

The overarching question is ‘how does individual plateau biodiversity/taxon assemblage vary between the rocky plateaus in the NWG?’ and then ‘what are the drivers of the differences?’ Within that:

- How do the focal taxa assemblages differ between study plateaus?
- Do they differ in a predictable way; for example with elevation or latitude?
- What is the relative role of the environmental clines in elevation, latitude and disturbance?
- What impacts do differing anthropogenic land-use changes have on the focal taxon assemblages?
- What patterns in distribution and drivers are consistent across all the focal taxa?'

The questions will be examined at a range of spatial scales from inter to intra-plateau and at a range of geographic distances.

Chapter 2. Islands within islands: the role of isolation, elevation and habitat in shaping water beetle assemblages across an archipelago of subtropical rocky plateaus.

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Author Contributions: CJT Designed and implemented the study and authored the paper: DTB assisted with study design, taxonomy and editing; SK assisted with fieldwork and logistics; JA assisted with data collection; AW assisted with permits and fieldwork; MEK assisted with study design, fieldwork and editing.

Abstract

Rocky plateaus are globally threatened ecosystems, and lateritic plateaus are frequent in the northern section of the Indian Western Ghats, globally one of the most important and threatened hotspots. These plateaus are known to support a diverse and highly endemic flora, but knowledge of their fauna, particularly invertebrates, is limited. During the monsoon, most plateaus support temporary rock-pool wetlands, which remain virtually un-investigated, in this area and in most parts of the tropics and subtropics. This study explored patterns of water beetle diversity and distribution sampling seasonal pools on 13 representative plateaus in western Maharashtra, across sites ranging from 67-1179m elevation, assessing the impact of environmental and anthropogenic drivers on assemblage composition. Beetle distribution was non-random at all levels of organisation and across all spatial scales. Assemblages differed significantly with elevation, latitude and land-use, with water temperature and rainfall frequency being the principal factors related to beetle distributions. Whilst human induced landscape changes appeared to affect water beetle distributions this effect was less important than other spatial explanatory variables. We conclude that for conservation purposes each plateau should be considered unique, findings likely to apply to these systems in other areas of the tropics and subtropics.

2.1 Introduction

Rock pools are amongst the oldest freshwater habitats worldwide (Jocqué, 2010), pools on rock outcrops typically making a significant contribution to levels of regional aquatic endemism (Pinder et

al. 2000; Jocqué, 2010). Many rocky plateaus, which support many rock pool complexes, are of recognised international biodiversity importance, being globally threatened ecosystems with high diversity and endemism due to their archipelago-like nature (Jocqué, 2010; Hopper et al. 2015; Porembski et al. 2016). Our knowledge of the biodiversity of plateau rock pool complexes, and the factors structuring their assemblages, remains limited, however, particularly in (sub)tropical regions (Pinder et al. 2000).

The Western Ghats/Sri Lanka Biodiversity Hotspot is one of the eight most important hotspots in the world and one of the three most threatened (Cincotta, Wisnewski & Engelman, 2000; Myers et al. 2000; Sloan et al. 2014). The Deccan Traps area of the northern Western Ghats (NWG) is a geologically and climatically distinct region (Fig 1.0-1, 2, 4), characterised by isolated hilltop plateaus formed from ferricretes of laterite (Widdowson & Cox, 1996; Watve, 2013). The patchily distributed plateaus are likely to function as habitat islands in a topographically heterogeneous landscape each with an individual environment derived from clines in edaphic conditions, rainfall and temperature (Davidar et al. 2007; Robin et al. 2012; Watve, 2013; Qian et al. 2014). Indeed, elevated levels of endemism have been demonstrated in a range of taxa, including plants (Lekhak 2012), and amphibians (Biju et al. 2009), whilst population genetic isolation occurs in macaques (Ram et al. 2015) elephants (Vidya et al. 2005) and birds (Robin et al. 2010). The scant soil cover over laterite derived from basalt on plateaus in the Ghats means they are rapidly transformed into seasonal rock pool wetlands on the arrival of the monsoon rains. Despite the extensive occurrence of these wetlands, our knowledge of their biota remains limited, although several species of large Branchiopoda have been reported recently including new taxa (Bharucha, 2010; Rogers et al. 2014). There remains an urgent need to better understand the factors structuring wetland assemblages in the region, in order to inform the conservation and management of these threatened ecosystems.

Aquatic Coleoptera make excellent surrogates of wider aquatic invertebrate biodiversity making them an ideal focal taxon for studying the comparative ecology of small wetlands, such as rock pools (Bilton et al. 2006; McAbendroth et al. 2005; Grantham et al. 2010). Pool selection and occupancy by beetles is dependent upon a range of physical and chemical factors including water temperature (Gioria, 2014), pH (Gioria, 2014), water chemistry (Valladares, 2002), dissolved oxygen (Verdonschot et al. 2011), pool size (Oertli et al. 2002), microhabitat availability (Valladares, 2002) and hydroperiod (Jocque et al. 2010), many of which vary with land use and disturbance (Lundkvist et al. 2001; Lundkvist, 2002; Picazo et al. 2012). European studies show that pool assemblages change during the hydroperiod, with high species turnover during filling, when the community comprises early colonisers, through to greater stability as pools start to dry and are occupied by species able to tolerate the poor water quality. To date, our understanding of these processes in (sub)tropical regions remains limited, however.

Water temperature shapes the occupancy patterns of aquatic beetles in small vernal pools (Gioria, 2014) and is a limiting factor in the distribution of ectotherms in general (Buckley et al. 2013) including water beetles (Calosi et al. 2010; Sánchez-Fernández et al. 2012). This may be particularly true for populations at low latitudes where their physiological adaptive limits are close to their environmental maxima (Pereira et al. 2017). Insects at low latitudes have a lower tolerance to warming and a narrower thermal safety margin that species at higher latitudes (Deutsch et al. 2008), Optimal fitness in tropical insects (6°N) has a much narrower range than their temperate counterparts and peaks ~28°C (Deutsch et al. 2008). Their adaptation to a narrow temperature band may restrict their ability to disperse vertically due to inter-site changes in temperature related to elevation (Janzen, 1967; Ghalambor et al. 2006; Archibald et al. 2013; IMD 2016; India 2017). Water beetles may avoid temperature extremes through behavioural mechanisms (Buckley et al. 2013). The temperatures they are exposed to in the study area are higher and less variable in the Konkan than above the escarpment (Watve, 2010; Watve, 2013).

This study explores factors shaping the water beetle fauna of rock pools on the lateritic plateaus of the northern Western Ghats, examining how assemblages are structured across a range of spatial scales, from individual rock pools to regions. With the objective of answering:

- Are all the western Maharashtan rocky plateau water beetle assemblages the same?
- If they differ ‘what are the environmental factors driving the distribution pattern?
- Then ‘do anthropogenic land-uses change water beetle distribution?

Given the global importance of aquatic habitats on rocky plateaus and the paucity of data for such systems in threatened regions of the tropics and subtropics, our study has wider implications for the conservation and management of such systems in many regions of the globe (Adams et al. 2013; Sutherland et al. 2017).

2.2 Materials and methods

2.2.1 Study area and Sampling design

The study area (Fig 1.0-4) includes 13 plateaus (Table 1.0-3) situated both above and below a North-South trending escarpment in the northern section of the 1600 km Indian section of the Western Ghats/Sri Lanka Biodiversity Hotspot. The plateaus are complex matrices of microhabitats and support a wide range of water bodies from seeps to deep pools, all subject to regular drying events (Watve, 2010; IMD, 2016; Thorpe et al. 2016). Rock pool diversity is strongly impacted by rainfall seasonality which in the NWG is highest along the crest line of the escarpment, with a declining latitudinal pattern in the number of wet days (Garrigues 1999; Brendonck et al. 2015; IMD, 2016; India, 2017). The number of wet days in the north of the study area is ~11% less than the south (IMD, 2016; India, 2017). The higher rainfall above the escarpment results in more consistent pool filling and the persistence of extensive shallow pools (India, 2017). The NWG plateaus are under pressure from proximate threats: localised threats such as illegal hunting, extraction of non-timber forest

products, livestock grazing, and fires, and landscape-level threats such as mining, road construction, hydro power projects, wind farms, large-scale agricultural expansion, creation of monoculture plantations, tourism and open cast bauxite mining (Cincotta et al. 2000; Phillips, 2012; Lad, 2013; Balaji et al. 2014; CEPF, 2016). To assess variation at differing spatial extents the study area was divided into r Regions separated by the Western Ghats escarpment and each Region was subdivided into three latitudinal sections creating 6 areas. These may be like life zones but are arbitrary being related to local factors and for the purposes here called Eco-zones (Holdridge, 1967).

To assess the spatial variation in the distribution of aquatic Coleoptera on the plateaus of western Maharashtra and their environmental drivers the 13 representative plateaus ranged from 67-1179 m a.s.l. (m) and covering more than 2° of latitude (15.89 to 17.92 °N) encompassing a range of land-uses (Fig 1.10-4; Table 1.0-3). Where possible sites were selected in pairs from each location to represent the differing land uses present. In the north of the High Region there is the largest expanse of laterite and 4 sites were surveyed here, with two different anthropogenic land-uses and a low disturbance reference site, as a control group. Six pools were selected on each plateau; the same plateaus were sampled in 2013 and 2014. Pools sampled were both natural and man-made, and ranged in depth from 50 mm to > 600 mm (Fig 2.0-1). To minimize inter-year variation in assemblage structure, sampling was conducted in the same weeks.

Figure 2.0-1. Pools are highly variable ranging from hygropetric seeps to small man-made lakes. Most plateaus have a range of pools from which a representative sample were survyed. These illustrations show a typical range of pool forms found on the lateritic plateaus with varying amounts of marginal and emergent vegetation.

Site geographic location and elevation (m) were recorded using a Garmin Map 60s hand held GPS (Garmin, Olanthe, KS, USA). Pool size, depth, and vegetation were all highly variable and pools were selected to encompass the range of sizes and microhabitats present on each plateau.

2.2.2 Water beetle sampling

Sampling was semi-quantitative, involving a 60 min search per pool, this commenced with a visual inspection of pool surface, margin and vegetation (10 min.) followed by 10 minutes washing exposed rock margins and searching hygropetric areas then 10 min disturbing the base of the pool by trampling to raise crawling species into the water column then immediately netting that area. The remaining 30 min was spent netting through open water and vegetation. A pond net with a 1mm mesh and a 242 mm opening was used.

Net contents were searched by hand on site using a white plastic tray and adult Coleoptera preserved in 99% ethanol in 2 ml plastic tubes. In the laboratory samples were subsequently sorted, counted, and identified to the lowest taxonomic level possible.

2.2.3 Environmental variables

Five physical and chemical variables were recorded at each pool: water temperature (°C), pH (Oaklon Instruments stick meter pHtestr 3+ or a Hanna Instruments stick meter model pHep, HI98128 stick meter); dissolved oxygen (% saturation) and water conductivity (µs cm^{-1}; YSI Instruments model YSI85-10FT; all instruments were calibrated before use).

Pool characteristics were assessed using nine metrics: maximum depth (mm); surface area (m^2); vegetation cover (% of margin and/or surface vegetated); water turbidity (visually scored using 0 completely clear - 5 fully obscured at a depth of 150 mm); substrate (rock, silt or mixed). Whether it rained during a survey was also recorded as an important microhabitat, surface flooding, only exists during rainfall and for a few hours after cessation. Anthropogenic disturbance in respect of land-use type and disturbance type were recorded. Intensity being scored using an arbitrary ranking system based on the number of disturbance factors observed on each plateau. Disturbance factors recorded

were; removal of loose rocks, surfaced road, unsurfaced road, built structures on the plateau, domesticated animal grazing, surfaced road within 200m of plateau, tourism, part conversion to plantation, adjacent built structures, importation of topsoil. Sites with 0-3 factors were considered to have low levels of disturbance, 4-7 Medium Disturbance, 8+ High Disturbance.

2.2.4 Data Analysis

Spatial autocorrelation in environmental and biotic data was first assessed by comparing Bray-Curtis and Sørensen similarity matrices with an inter-site distance matrix using the RELATE routine in Primer-e v7, with 999 randomised permutations (Legendre, 1993; Legendre et al. 2002).

The impact of latitude, elevation, climate and microhabitat on pool environment and water beetle distribution in the study area was assessed for each of the spatial sub-units: pool, plateau, Eco-zone, Region and elevation and latitude.

To assess the impact of the spatial sub-units on the environment the ANOSIM routine in Primer-e v7 was performed on a Euclidian Distance matrix of square root transformed pool data using a crossed design of plateau within each of: Region, Eco-zone, Elevation and Latitude (Clarke et al. 1988; Clarke et al. 2015).

Macro-scale biotic relationships were initially investigated in a series of Permutational Manova's (Permanova) performed on Bray-Curtis matrix of square root transformed data incorporating an environmental covariable as eigenvalues from the significant axes of a Principal Component Analysis (PCA) in Permanova+ for Primer-e v7, (Permanova) (Jolliffe 2002; Anderson et al. 2008). As some spatial units had low numbers of observations, Monte Carlo permutation tests were used to generate a Pseudo *F* statistic and *P* (MC) values, tests with lower than 95% confidence intervals are not reported.

To assess the relative importance of each spatial element in the Permanova, the square root of the estimates of the components of variation were compared as the % of variation explained (Underwood et al. 1993, Anderson et al. 2008). To confirm the validity of spatial groups, and to identify the principal taxa driving patterns, a canonical analysis of principal coordinates (CAP) was conducted on the *a priori* groups Latitude Groups and Elevation Groups. This seeks explanatory axes in the multivariate data cloud for *a priori* groups (Permanova+, Primer-e v7; (Brokovich et al., 2008; Anderson et al. 2003). The CAP analysis was performed on a Euclidian Distance matrix and as such can be considered an expression of beta diversity in the study area (Legendre et al. 2005).

To explore the possible impact of individual environmental factors on biotic distributions DistLM, a distance based multiple linear regression model, was used. Permutation tests were performed in Primer-e v7 (Legendre et al. 1999; McArdle et al. 2001; Anderson et al. 2008). Environmental explanatory power was assessed with non-metric multi-dimensional scaling ordination (nmMDS) of Euclidian Distance matrices of normalised data (Kent, 2012; Clarke et al. 2015).

Spatial patterns in beetle assemblages were assessed at the pool, plateau, Eco-zone and regional scales. The impacts of elevation, latitude and microhabitat on total abundance, species number, Inverse Simpson's Index (1-D) and Pielou's J' were assessed using Pearson Product Moment or Spearman Rank correlations in Minitab™ v17. Spatial turnover was examined via Whittaker's Beta diversity index (β_w) using the formula: ($\beta_w = \frac{S}{\overline{a}} - 1$) where S = total types in the region and $\overline{a}$ average site sample species number, calculated in PAST software (Whittaker, 1960; Hammer et al. 2001).

To assess the impact of anthropogenic land-use and disturbance on beetle assemblages, the ANOSIM routine in Primer-e v7 was performed on a Bray-Curtis similarity matrix of square root transformed pool data (Clarke et al. 1988; Clarke et al. 2015). To compare land use types, a metric multi-

dimensional scaling (mMDS) analysis was performed on a rank distance matrix constructed from the ANOSIM R value matrix (Anderson et al. 2008). The SIMPER routine was used to generate pool similarity percentage values within each disturbance class (Primer-e v7; Clarke et al. 2015).

2.3 Results

2.3.1 Spatial structuring in the environment

Pool environmental data were not significantly spatially auto correlated (RELATE, P>0.05). All five physical and chemical variables were correlated with elevation (two negatively) together with three additional environmental parameters (Table 2.0-1). Rainfall frequency was 12.7 times higher above the escarpment than below it. Mean water temperature was 7.4°C higher in pools below the escarpment, with a notable high of 36.4°C (Table A.1.3). Pool pH varied, with low sites acidic and high sites alkaline (Table A.1.1). Only 4.8% pools had pH <5.5, 95.2% pH>5.5; 65% of pools had pH<6.5. Water conductivity was low but variable, ranging from a minimum of 2 - 63.9 µS/cm (Table A.1.3). Mean dissolved oxygen concentration was higher above the escarpment, but highly variable and not significantly different from that observed below the escarpment (Table A.1.3). Only turbidity and the percentage of vegetation in pools and on their margins displayed weak, but significant, correlations with latitude ($0.03 < r^2 < 0.07$; $P < 0.05$).

Table 2.0-1. Correlation between elevation and environmental variables. Pearson Product Moment correlation with confidence interval. Non-significant correlations have been excluded.

Variable	r^2	**P**
Pool Water Temperature	-0.822	<0.001
Rainfall frequency	0.645	<0.001

Water Conductivity	-0.427	<0.001
pH	0.244	<0.001
Pool Surface Area	0.234	<0.05
Pool base - Rock	0.168	<0.05
Turbidity	0.167	<0.05

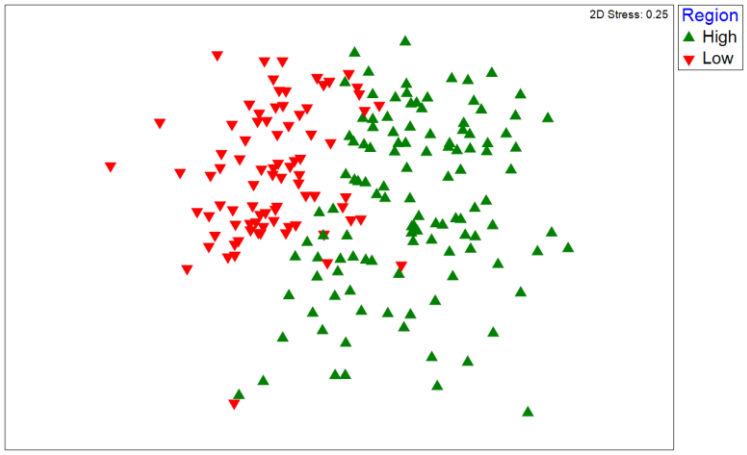


Figure 2.0-2. nmMDS ordination for all pool environmental data in a Euclidian Distance matrix analysed for Regions, High and Low.

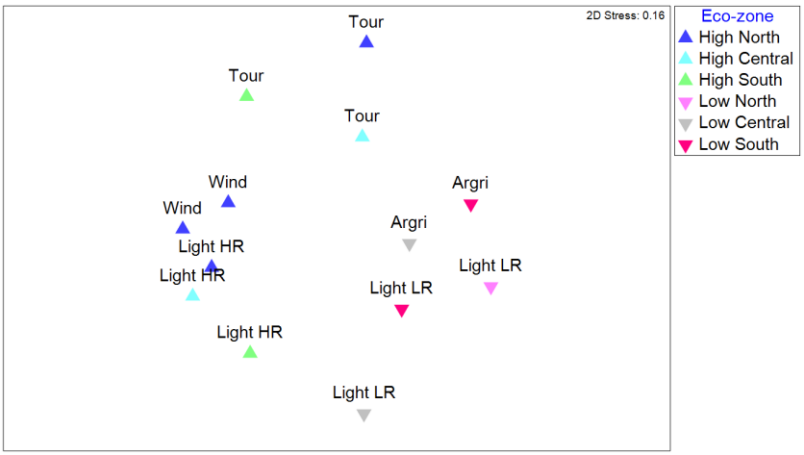


Figure 2.0-3. nmMDS ordination for mean site values for square root transformed pool abiotic data in a Euclidian Distance matrix analysed for Eco-zones with land use shown to illustrate the impact of land-use on elevation and latitude derived changes. Land-use classes: Agri-agriculture; Light HR-low disturbance site in the High Region above the escarpment; Light LR-low disturbance site in the Low Region below the escarpment; Tour-tourism; Wind-wind turbine installation.

Pool environments were most dissimilar along a latitudinal gradient ($R=0.308$, $P<0.05$) compared to elevation, Region ($R=0.184$, $P<0.01$) or Eco-zone ($R=0.151$, $P<0.01$ [Fig 2.0-2 & 2.0-3]). The combined impact of the factors was explored through ordination finding, sites within the 6 Eco-zones, nmMDS generally cluster according to their elevation and latitude (Figs. 2.0-3). High Region sites are situated in the left of the plot in Fig. 2.0-3, with Low Region sites concentrated towards the right. The ordination also shows that High North sites, towards the centre-left of the plot, are more similar environmentally than sites in other Eco-zones except for Panchgani, a site with tourism. Panchgani is placed to the top-centre of the plot with another tourism site from the opposite end of the survey area (Amboli).

2.3.2 Distribution patterns in the biota

A total of 987 individual beetles were collected across the three years, belonging to 44 taxa from five families: Gyrinidae (3); Haliplidae (1); Noteridae (3); Dytiscidae (22) and Hydrophilidae (15), (Table A1.1 & 2). Variation in beetle assemblages was independent of the spatial arrangement of sites (RELATE, $P>0.05$).

2.3.3 Macroscale patterns

The area above the escarpment (High Region) held more individuals, more types and more genera than the area below the escarpment. Mean pool abundance within a plateau was greater above the escarpment but mean pool alpha diversity was lower (Table A.1.3 & 5). Pools were marginally more diverse (1-D) below the escarpment (0.624-0.567).

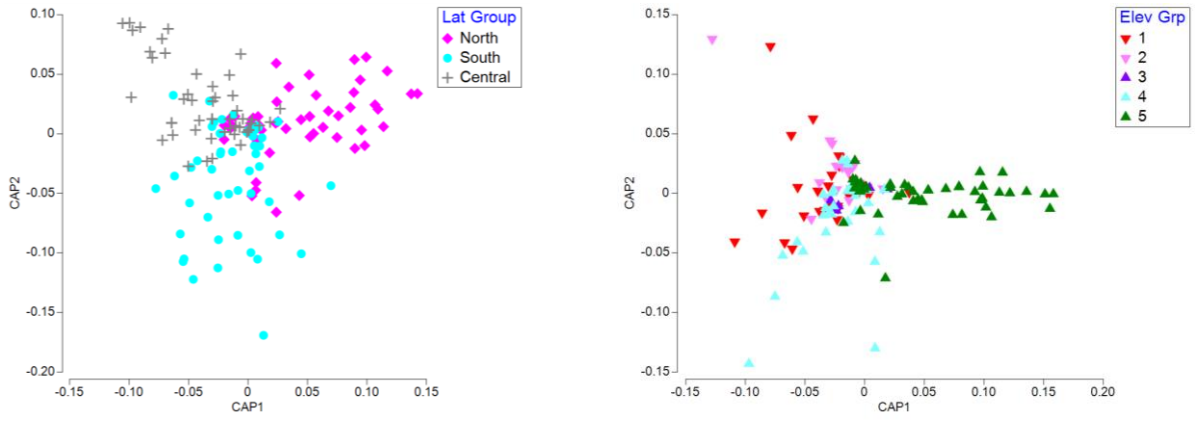
Only PC1 of the 5 component PCA of environmental data was found to be significant in the first Permanova, explaining 20.3% of variation. Only PC1 was carried forwards to subsequent Permanova analyses. Permanova Components of Variation, reported in Table 2.0-2, found All Taxa and Hydrophildae assemblages were most dissimilar at the lowest spatial scale, that of individual pool (27% and 29% respectively). Elevation and Latitude explained the highest amount of inter-pool variation in Dytiscidae (28% and 29% respectively), with Pool being close at 26%. Elevation and Latitude explained similar amounts of variation in hydrophilid assemblages (20% and 21% respectively). Region (as High and Low) had low explanatory power overall, as did latitude within North, South and Central areas (Table 2.0-2). The first axis of the Environment PCA, which explained 20.3 of the total variation, had low explanatory power for All Taxa, Hydrophilidae and Dytiscidae (6%, 6% and 5% respectively), despite 7 of the 9 abiotic variables being correlated with elevation (Table 2.0-2).

Table 2.0-2. Significant Permanova results for the macroscale factors structuring water beetle distribution. For Environment the eigenvalues from PC1 of a PCA of all habitat and environment variables was used as a covariable in the Permanova. Region refers to the two Regions split by the escarpment, Latitude Grouped is the area divided into three North, Central and South. Elevation refers to the height above sea level for the individual plateaus in the series of Permutational Manova's, (Permanova+, Primer-e). Both the F and P values were calculated from Monte Carlo permutation tests. The square root of the estimate of component of variation is expressed as a % and annotated C of V.

Unit of Comparison	**Pseudo F**	**P (MC)**	**C of V**
	All Taxa		
Environment PCA	17.521	0.001	6
Region	13.124	0.001	10
Elevation	15.355	0.001	25
Latitude Grouped	12.721	<0.01	11
Latitude, Individual Sites	11.711	0.001	21

Pool (Residual)			27
	Hydrophilidae		
Environment PCA	17.263	<0.01	6
Region	13.159	<0.01	11
Elevation	8.4932	<0.05	20
Latitude Grouped	12.101	<0.05	12
Latitude, Individual Sites	9.7621	<0.05	21
Pool (Residual)			29
	Dytiscidae		
Environment PCA	33.238	0.001	6
Region	23.527	<0.01	10
Elevation	37.937	<0.01	28
Latitude Grouped	22.995	<0.01	10
Latitude, Individual Sites	22.48	<0.01	21
Pool (Residual)			26

The results of the CAP analyses are shown in Fig. 2.0-4 a & b and Table 2.0-3. The distance between data points on the plot is proportional to the differences in the water beetle assemblages at each site. Whilst there is some overlap, pools in each group are separated. The main taxa impacted by these environmental clines vary and are reported in Table 2.0-3.



a) b)

Figure 2.0-4 a & b. CAP analysis of a Euclidian Distance matrix to illustrate the ordination of: a) latitudinal and b) elevational groups of pool data. Elevation groups: 1-0-100; 2, 100-200; 3, 700-850; 4, 850-1000; 5, 1000-1200 m.

Table 2.0-3. The 3 taxa principally responsible for the patterns in the CAP Discriminant Analysis (CP=CAP), CAP 1 and 2 indicate the axes in Fig. 4. a & b. Ele.-Elevation as 5 groups, Lat. as 3 groups including both high and low sites. Derived from Pearson Correlation matrix with a r >0.4 cut off. Dytiscidae (D), Hydrophilidae (H).

Taxa

Ele. CP 1	*D. Microdytes* cf. *belli; D. Cybister* sp.*; H. Regimbartia* cf. *attenuata*
Ele. CP 2	*H. Hydrobiomorpha spinicollis* ssp.*; H. Berosus* cf. *enopleuru;, H. Regimbartia* cf. *attenuata*
Lat. CP 1	*D. Microdytes* cf. *belli; D. Hydrovatus sp,; D. Cybister sp.; H. Regimbartia* cf. *attenuata*
Lat. CP 2	*H. Helochares* sp.*; H. Regimbartia* cf. *attenuate; D. Hydrovatus* sp.

2.3.4 Taxon distribution and environmental drivers

The DistLM routine identified the explanatory environmental factors which differed between water beetle families (A.1.4). Water Temperature, Dissolved Oxygen concentration and Rainfall Frequency were the most significant factors shaping the distribution of All Taxa and Dytiscidae. Hydrophilid assemblages were related to Water Temperature and Conductivity, Rainfall frequency and Turbidity. For Gyrinidae only the amount of Marginal Vegetation was significant.

2.3.5 Spatial Patterns in diversity

Differences in abundance (number of individuals), alpha (number of types in a pool or on a plateau), beta (β_w) and gamma diversity (number of types in a Region) are detectable at most spatial scales.

Water beetles were more abundant in the High Region than the Low Region and in-pool abundance was positively correlated with elevation both overall (ρ = 0.134 (P=0.069) and within the High Region (ρ = 0.212, p<0.05) (Table A.1.5). The number of pools and plateaus varied between Regions. When corrected for sampling effort, the High Region had almost double the number of individuals per plateau on each sampling occasion. High Region 35.1 compared to the Low Region's 15.7. A comparison of maximum in-pool abundance is more dramatic; High Region 62, Low Region 14. In-pool abundance declined with latitude below the escarpment (ρ = -0.248, p<0.05), and increased with the concentration of dissolved oxygen overall (ρ=0.290, P<0.001).

Inverse Simpsons Diversity index declined with elevation (ρ=-0.194, P<0.05) and weakly with latitude (ρ=-0.162, P=0.07; Table A.1.3). Pool communities became less even (Pielou's J) with increasing elevation (ρ=-0.251, P<0.01). Inverse Simpsons Diversity index was significantly correlated with pH (ρ=0.223, P<0.05) and weakly with pool depth (ρ=0.148, P=0.09; S1 Table 1). In-pool community evenness (Pielou's J) was negatively correlated with the concentration of dissolved oxygen and rainfall during survey (ρ =-0.272, P<0.01; ρ=-0.226, P<0.05 respectively).

Mean in-pool alpha diversity was greater in the High Region (2.23) compared to the Low Region (1.83 [App. 1, Table 3]). Alpha diversity declined with latitude (ρ = -0.495, P=0.086) and above the escarpment (ρ = -0.714) (Fig 2.5; Table A.1.3). Alpha diversity increased with the concentration of dissolved oxygen in the water (ρ=0.145, P<0.05).

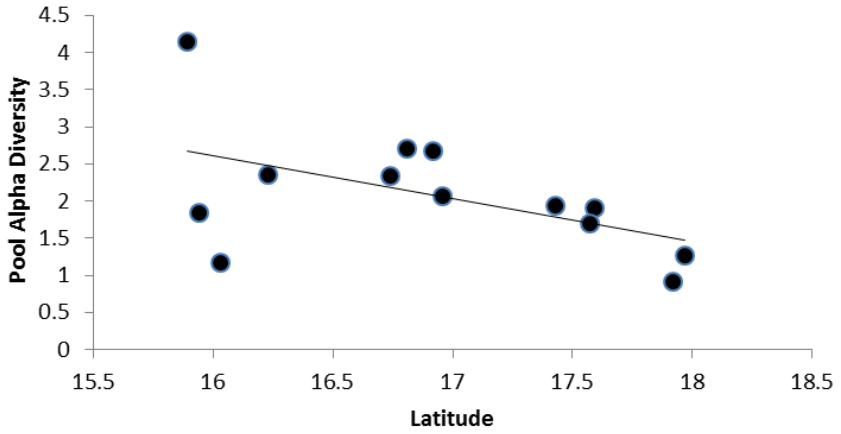
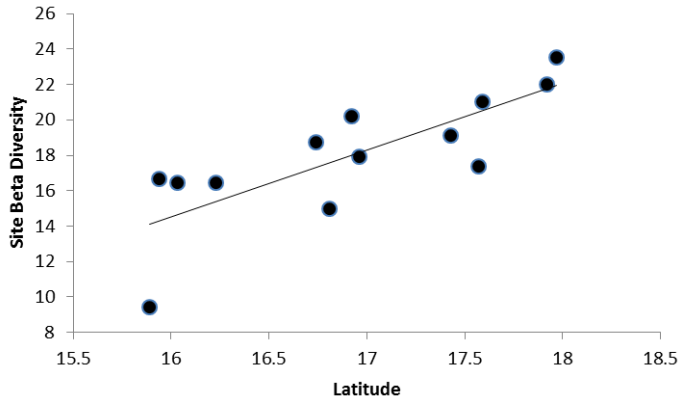
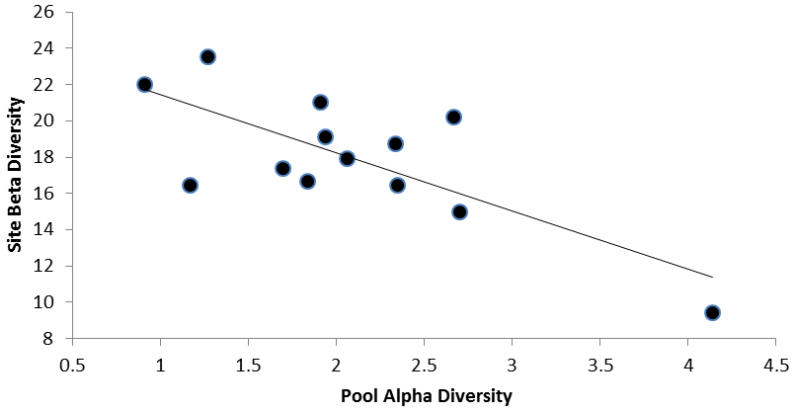


Figure 2.0-5. Pool alpha diversity as mean number of species in a pool within a Site related to that sites latitude.

Site diversity (β_w), increased significantly with latitude overall (ρ=0.834, P<0.001) and in each Region individually (Low ρ=0.872, P0.05; High ρ=0.881, P,0.01). High Region beta diversity (β_w) was positively correlated with elevation which increased with latitude (ρ=0.834, P<0.001). Beta diversity declined with increasing alpha diversity (ρ=-0.5, P=0.08).



a)



b)

Figure 2.0-6. Whittaker's Beta diversity (βw) values for plateaus plotted against a) Latitude in °N; b) mean plateau in-pool alpha diversity.

Gamma diversity was greater above the escarpment (44) than below it (32). This regional difference was also seen in exclusive taxa; the High Region had 12 types not found below the escarpment compared to the Low Region's 2 not found above the escarpment.

2.3.6 Impact of anthropogenic disturbance on water beetle assembalges

SIMPER in-pool similarity peaked at a mid-disturbance value (R^2=0.321, S=7.9; Fig 2.0-8) with Alpha diversity declining (ρ=-0.41, P>0.05) as disturbance intensity increased (Fig 2.0-7). There was no impact of disturbance on abundance or Beta diversity. Assemblages did not vary significantly with disturbance type (ANOSIM; R=0.178, Sig. 0.8%).

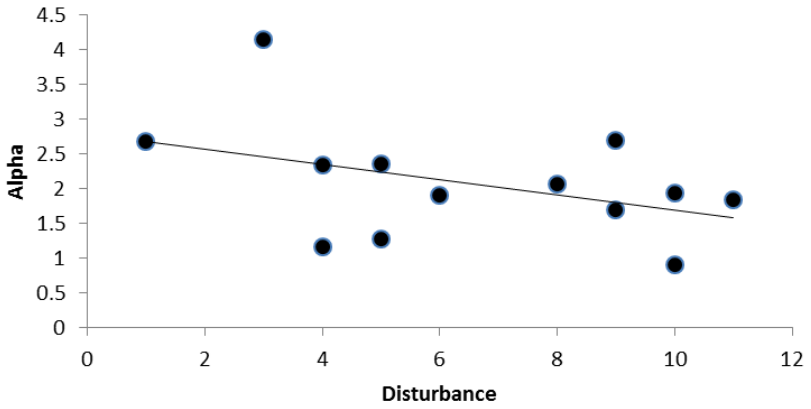


Figure 2.0-7. Alpha Diversity, the mean number of pool taxa on a plateau related to disturbance intensity. The descriptors of disturbance Low, Medium and High were transformed into numerical values for comparative purposes.

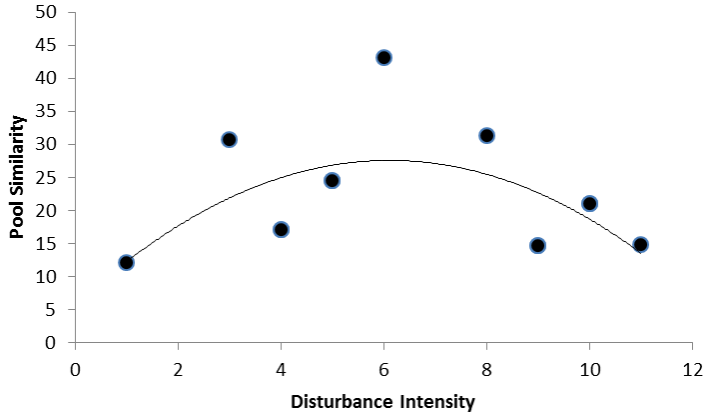


Figure 2.0-8. Site disturbance related to the square root of mean pool similarity (SIMPER) on each site. Site disturbance intensity: Low, Medium and High had been transformed into numerical values for comparative purposes. R^2 values are for 2rd order polynomial regression.

However, disturbed sites are distant from all non-disturbed ones on the mMDS (Fig 10). The installation of windturbines would appear to have the greatest impact on assemblages in the study area (Fig. 10).

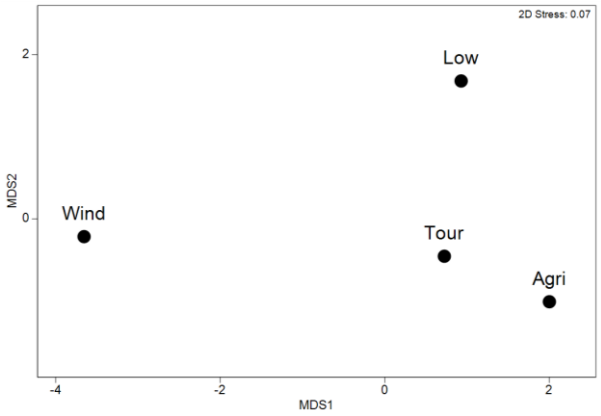


Figure 2.0-9. mMDS ordination of a rank distance matrix for land use classes, constructed from the pairwise R values from an Anosim analysis of a Bray-Curtis similarity matrix. Low-Light Disturbance; Wind-sites with wind turibine installations; Tour-sites with tourism; Agri-all agricultural uses.

2.4 Discussion

2.4.1 The biogeography and diversity of aquatic Coleoptera

The distribution of aquatic Coleoptera in the rock pools on the rocky plateaus in western Maharashtra was non-random at all levels of organisation and at all spatial scales. Abiotic changes linked to elevation were the principal drivers of the spatial patterns seen, but with a strong latitudinal cline in beta diversity. Pool water temperature and rainfall frequency were the strongest drivers, but at a family level different secondary environmental driver were identified. The greatest differences in assemblages were typically observed at the finest scale, i.e. between pools. The species impacted by elevation were different from those impacted by latitude in the CAP analysis. Disturbed sites had lower alpha diversity that undisturbed ones, with in-pool community similarity peaking at a mid-

disturbance level. Anthropogenic land-use type and disturbance intensity impacted distributions, but the effect was weaker than that of the spatial explanatory variables. Wind turbine installations appeared to have the greatest impact, followed by agriculture then tourism when assemblages were compared to low disturbance reference sites.

2.4.2 Spatial structuring in the environment drives water beetle distribution

Elevation and latitude *per se* do not regulate taxa distribution; rather it is individual species responses that drive the pattern (Jacobsen et al. 2008; Verberk et al. 2011; Moura et al. 2016). This study demonstrates spatial structuring in pool environments with both elevation and latitude. All the abiotic variables measured are known to impact water beetle distribution (Gioria 2014). It should be remembered that elevation increases with latitude above the escarpment, 809-1131 m but only 85-170 m below it as well as west to east in all parts of the study area. Not only elevation but topographical complexity increases with both elevation and latitude in the High Region (Widdowson & Cox 1996). Such landscape complexity creates a thermally diverse landscape with possible dispersal barriers present between higher elevation sites (Ghalambor et al. 2006; Laurance et al. 2011).

Both elevation and latitude had a similar level of impact on beetle distributions, with different species driving the elevation and latitude patterns. Over the study's elevational range of 65-1131 m we found that alpha diversity increased with elevation, peaking at 854m before declining in line with (Valladares 1990) who found a peak at 700-1100 m and (Rahbek 1995) 500-1000 m. We also report a differential macroscale difference in the distribution of individual families as they respond individually to separate abiotic drivers, with 82% of Dytiscidae found in the High Region compared to 62% of the Hydrophilidae supporting a Tunisian study which found Dytiscidae richness increased with elevation 1.6 times faster than that of the Hydrophilidae (Table A.1.2; Touaylia 2011). We found in-pool abundance positively correlated with elevation up to 1179 m, with the higher pools dominated

by a limited number of abundant small Dytiscidae with low diversity resulting in an elevational decline in Simpson's Diversity index.

Water temperature and rainfall frequency had the greatest explanatory power in the environmental PCA. Water temperature was the most important driver of distribution for both Dytiscidae and Hydrophilidae in the study. It is widely recognised as being highly important in structuring ectotherm distributions and aquatic invertebrates, as it has a regulatory effect on oxygen availability as well as a direct physiological impact (Verberk et al. 2011). Whilst water temperature in Low Region pools is high, peaking at 36.4° C, it is well within the lethal maximum reported for water beetles in a Mediterranean system (~54°C; (Arribas et al. 2012), although how these tropical taxa compare is unknown. Temperatures well below lethal thermal limits can lead to fitness reduction and in tropical invertebrates this is reported to occur at ~30° C (Deutsch et al. 2008). We therefore suggest that thermal exclusion may be a possible explanation for the lower number of species in Low Region pools.

2.4.3 Pool physical parameters

Rainfall frequency, the second most important driver of environmental pattern, was significant for both families. It was significantly higher above the escarpment and delivers 11% more wet days in the south, thus regulating both pool type and hydroperiod. We suggest that pool profile is one of the distributional drivers supporting the findings of Ribera et al. (1995). Pools with a larger surface area were more common in the High Region where the intensive rainfall not only fills pools but creates extensive surface flooding that are reliant on continuity of rainfall (IMD, 2016; India, 2017). Pools with a rock substrate were also more abundant at high elevations; Ribera et al. (1995) suggest such pools are suited to small to medium sized beetles with a spherical body shape. Our analysis identified two such species as being distributed by elevation *Dytiscidae Microdytes* cf. *belli* and *Hydrophilidae Regimbartia* cf. *attenuata.* They identify deeper pools with free swimming species such as

Hydrophilidae Hydrobiomorpha spinicollis ssp. and *Dytiscidae Cybister* sp. associated with the elevational pattern in the CAP analysis. Pool water conductivity, which declined with elevation, was the second most important factor in the distribution of the Hydrophilidae after water temperature, their abundance increasing with declining conductivity. Turbidity increased with elevation and was important in the Hydrophilid distribution. Their distribution was split, with 38% below the escarpment and 62% above. Water conductivity is widely recognised as being important in structuring aquatic coleopteran assemblages (Valladares et al. 2002; Picazo et al. 2012), although it is typically reported to have a positive relationship with species richness, a finding this study does not concur with.

Dissolved oxygen concentration was the second most important physical and chemical parameter, after water temperature, in the distribution of Dytiscidae. It was greater in the High Region pools and was positively correlated with in-pool abundance and alpha diversity, but negatively with community evenness. It was particularly important in the distribution of Dytiscidae which are more abundant and diverse in the High Region (Table A.1.2). Oxygen availability declines with elevation more rapidly than mean weight-specific respiratory rates which implies a potential oxygen deficiency although the surveyed elevational range may be too limited to be impacted (Jacobsen et al. 2003). Mechanisms are likely to include genera specific oxy-regulation and respiratory mechanisms (Ribera et al. 1995; Jacobsen, 2008; Verberk et al. 2011).

Gyrinid distribution was related to a single abiotic variable, the percentage of pool margin with Emergent Marginal Vegetation. Emergent rather than submerged vegetation is important for some species (Nakanishi et al. 2014) and Emergent Marginal vegetation is an essential element in the presence of some species (Landin, 1976).

pH increased with elevation and was correlated with Simpson's Diversity Index. The pool pH values exceeded the pH of regional edaphic conditions produced by the acidic oxisols (pH4.5-5.9 [Dikshit,

2002]) and plateau soils pH4.9 (Watve, 2010). One possible explanation for pH increasing with elevation most pools being above the soil pH may lie in the flushing effect from rainfall. Whilst some species are tolerant of a wide pH range, others have specific pH requirements (Gioria, 2014). The specific response to pH may cause the exclusion some species when pH falls below 5.5 (Friday, 1987) or 6.5 (Picazo et al. 2012). Both Regions had pools below those thresholds; the Low Region had a minimum pH (4.9) and the High Region (5.3).

2.4.4 Latitudinal variations in pool biota

Latitude had a significant effect on the distribution pattern of water beetles in this study but like elevation it has no direct effect, rather it is a useful metric to refer to a suite of abiotic variable that change with it. However, as elevation increases south to north above the escarpment it is more problematic to disentangle the impact of latitude from elevation. The one variable independent of elevation is seasonality, which has a south to north cline in the study area with 11% more dry days on the northern sites, resulting in a hydroperiod gradient along which species assemblages are known to vary (Jocque et al. 2010). Pool drying is an extreme and recurrent disturbance event for aquatic invertebrates and only those adapted to survive the dry period survive (Florencio et al. 2016). As we found, more ephemeral pools are reported to have low species richness, having selected for species that are early colonisers or have short life cycles (Studinski et al. 2007).

Beta diversity increases strongly with latitude in the Low Region, despite there being little change in elevation. A comparable situation exists in the High Region, where there is an increase in elevation, suggesting the effect is independent of elevation-related environmental variables. We propose rainfall seasonality as the driver here, with the northern sites receiving approximately 11% less wet days per monsoon. Hydroperiod is well known to be important in water beetle distribution with pools having a shorter wet phase often displaying higher beta diversity (Florencio et al. 2016). A strong relationship

between alpha and beta diversities exists with both related to the cline in elevation and the species assemblage changed with elevation and latitude.

2.4.5 The impact of anthropogenic disturbance on the distribution of water beetle assemblages.

The highest sites in the High North Eco-zone have a three land-uses and are relatively close together in elevation and geographical distance yet are widely spaced in the nmMDS and mMDS plots suggesting at this scale land-use may be an assemblage driver (Dinakaran et al. 2007; Qian et al. 2014). In this study individual pool communities were most similar at an intermediate level of disturbance, with the sites with the lowest disturbance having the least even assemblages, with the exception of Amboli High which reflected the assemblage of its close neighbour Amboli Low, a site with high levels of tourism. Alpha diversity declined with disturbance intensity (Fig. 2.6b). Wind Turbine installations appear to have the greatest impact on water beetle assemblages in the mMDS analysis contrary to the findings of Millidine et al. (2015), with Tourism and Agriculture the least when compared to low disturbance reference sites. However, High Region sites with tourism had alpha diversity values 55% lower than the low disturbance sites closest to them. That impact is often most acute on rare species and as most taxa in the study were singletons, their distribution in the wider landscape is unknown (Sánchez-Fernández et al. 2008). Disturbance frequency is reported to impact water beetle assemblages and appears to have changed plateau communities, but the mechanism is unclear (Colombini et al. 2011; Vanschoenwinkel et al. 2013).

2.5 Conclusion

The study finds that rock pool water beetle assemblages on the lateritic plateaus in the northern Western Ghats Biodiversity Hotspot are highly individualistic within and between sites. The study data increases our knowledge of the ranges, ecology and distribution of aquatic Coleoptera in the area

considerably. In contrast to their historical definition as barren wastelands, the study demonstrates that these plateaus are significant reservoirs of freshwater biodiversity. Most taxa were locally rare in the study and many demonstrate very limited distributions. Many of their microhabitats are exclusive to the lateritic plateaus therefore they are essential for the preservation of their rare aquatic biodiversity (Baillie et al. 2004). The study supports Hero et al. (2008) in that these habitats need conserving *per se* but we further demonstrate that land-use impacts aquatic Coleoptera which are good surrogates of other freshwater biodiversity and therefore such changes should require informed assessment before development is permitted.

Chapter 3. Amphibians: Drivers of amphibian distribution on the poorly understood rocky plateaus in the Western Ghats, India, biodiversity hotspot: implications for conservation.

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Author contributions: CJT Designed and implemented the study and authored the paper: TRL assisted with the study design, data collection, taxonomy and editing; DTB assisted with study design; SK assisted and logistics; DP and LD assisted with data collection; DTB assisted with study design, taxonomy and editing; AW assisted with permits and fieldwork; MEK assisted with study design and editing.

Abstract

This study is the first quantitative comparative investigation of the distribution drivers of rocky plateau amphibians in the northern Western Ghats, India. Rocky plateaus and in particular basalt derived lateritic plateaus are rare and globally threatened ecosystems. Amphibians are a globally threated group and those endemic to vulnerable ecosystems are in double jeopardy. These plateau ecosystems are frequent in the northern section of the Western Ghats, globally one of the most important and threatened biodiversity hotspots. Most plateaus can be characterised as seasonal wetlands during the monsoon which remain virtually un-investigated biologically. We compared quantitative amphibian samples from 13 representative plateaus in western Maharashtra, from sites ranging from 67-1179 m elevation, assessing the impact of the environment and land-use. Amphibian distribution was individualistic at site scale with higher elevation sites most distinct. The amount of

woody plants, ponds and water conductivity drove anuran distribution with streams, rainfall frequency, loose rock abundance and pH important to caecilians. Sites with anthropogenic land-use contained a greater proportion of generalist or disturbance tolerant species most notable on plateaus with tourism or wind turbines. A Bergmann cline was identified in both amphibian families. We conclude that for conservation purposes each plateau should be considered unique and the impact of changes in land-use planned.

3.1 Introduction

Effective amphibian conservation is dependent upon an understanding of the factors necessary for each species survival (Adams & Sandbrook, 2013; Sutherland & Wordley, 2017). Here we present the first comparative quantitative study of the amphibian distribution drivers on the threatened rocky plateaus in the northern section of the Western Ghats Biodiversity Hotspot in India (WG) (Fig 1.0-1 & 3). Amphibians are a globally threatened group at risk from: disease, land-use changes, pollution and climate change (Hof et al. 2011). There is an urgent need to understand the ecology and distribution drivers of those endemic to scarce and threatened ecosystems such as the rocky plateaus in southwest India (Humraskar & Velho, 2007; Watve, 2013; Porembski et al. 2016).

The Western Ghats-Sri Lanka Biodiversity Hotspot (WG) is both one the eight most important global hotspots and one of the three most threatened by human population growth (Cincotta, Wisnewski & Engelman, 2000; Sloan et al. 2014). Rocky plateaus (plateaus) characterise the northern section of the WG (NWG), they are of international importance for their substantial contribution to regional biodiversity and endemism (Fig 1.0-2 [Pinder et al. 2000; Jocque, Vanschoenwinkel & Brendonck, 2010; Porembski et al. 2016]). Within India they are recognised as fragile and threatened ecosystems which are being destroyed and damaged extremely rapidly through human activity (Bharucha, 2010; Kasturirangan et al. 2013; Watve, 2013; Porembski et al. 2016).

Rocky plateaus and their aquatic systems are now recognised as globally important systems due to their elevated levels of unique and endemic taxa (IUCN, 2012; Dalu, Wasserman & Dalu, 2016; Hopper, Silveira & Fiedler, 2016; Porembski et al. 2016). However, those in NWG have historically lacked protection being inappropriately mapped as 'wastelands or rock outcrops' because of their barren appearance for much of the year, despite their unique ecosystem being recognised at state and national level (Bharucha, 2010; Watve, 2010; Kasturirangan, et al. 2013; Watve, 2013). Proximate threats include; bauxite mining (Porembski et al. 2016; Thorpe & Watve, 2016); tourism (Watve, 2013); loss of habitat and development (Bharucha, 2010; Kasturirangan, et al. 2013) and infection (Molur et al. 2015). Due to their lack of recognition they received little attention from ecological researchers until the early 21st century (for example Porembski & Watve, 2005; Lekhak, 2012; Watve, 2013). The monsoon changes their dry barren appearance into a vegetated and exceptionally wet environment with surface flooding. Ephemeral flush vegetation dominates with many floral species adapted to low nutrient and highly stressed environment (Porembski & Watve, 2005; Hobbhahn, Küchmeister & Porembski, 2006; Watve, 2013). Their flora has elevated levels of species richness (35%) and endemism (19%) but more importantly 58% of these endemics are only found on plateaus (Lekhak, 2012). The NWG has 5 monotypic floral genera and many species with very limited distribution 34 of the endemics are Critically Endangered, 18 Endangered and 20 vulnerable (Gaikwad et al. 2014).

That floral diversity may be reflected in the NWG amphibians. We know little of individual amphibians ranges and ecology in the NWG we infer from the WG as a whole but see (Gaitonde & Giri, 2014; Padhye, 2014; Gaitonde, Giri & Kunte, 2016). If the three sections of the WG are combined 87% of amphibian species are endemic and the WG are home to 39% (161) of India's amphibian species (415) in just 5% of India' land area making the WG the most amphibian species rich region in the country (Aravind & Gururaja, 2011; Dinesh et al. 2017). Some, including species found on the plateaus, are known to be critically endangered, endangered or data deficient (Biju et al. 2009; Padhye, 2013; Giri, 2016; IUCN, 2016-2). Amphibians are a globally threatened group (Hof, et

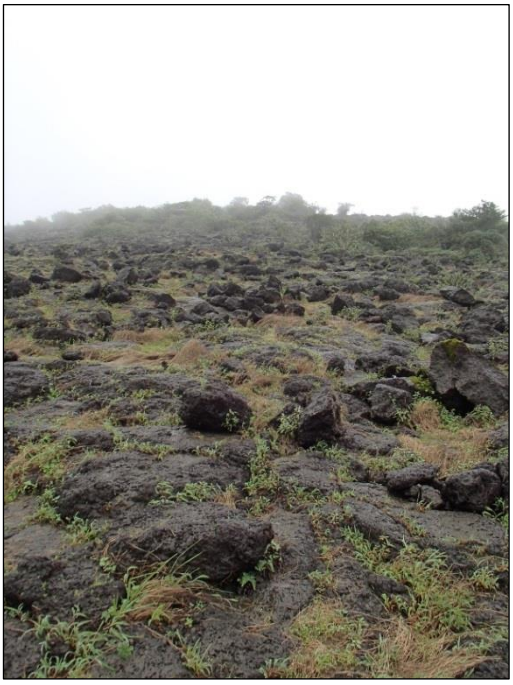
al. 2011) with those of the NWG exposed to both the global risks and localised threats from land-use changes (Kasturirangan et al. 2013; Mittermeier et al. 2011; Thorpe & Watve, 2016).

a)

b)

c)

d)



e)

f)

Figure 3.0-1 a-e. Illustrations of inter-season and land-use plateau variability. Images a & b early monsoon horse riding for tourists with man-made lake in the centre of b. Images c & d illustrate low disturbance sites in early monsoon with abundant loose rocks. Images e & f are from, early dry season sites with wind turbine installations.

The WG have high topographical heterogeneity which has resulted in population genetic isolation in macaques (Ram et al. 2015), elephants (Vidya et al. 2005) and birds (Robin et al. 2010). Isolation and divergent stressors in the NWG has driven endemism in a range of taxa, including plants (Lekhak, 2012), amphibians (Biju et al. 2009; (Padhye, 2013) and reptiles (Giri et al. 2017). The isolated hilltops south of the study area are described as sky island refugia for birds (Robin, Sinha & Ramakrishnan, 2010). It is expected the (sub)tropical plateaus in the NWG will show similar isolation especially for taxa such as amphibians with low dispersal ability and acclimated to narrow temperature bands (Janzen, 1967; Ghalambor et al. 2006; Barker, Rodríguez-Robles & Cook, 2015). High elevation taxa are often more diverse than those of lower elevations (Navas, 2002) because of topographical isolation (Ghalambor et al. 2006) and elevational specialism (Laurance et al. 2011). Sixty per cent of tropical amphibians in an area can be high elevation specialists (Laurance et al, 2011) with beta diversity a useful metric (Laurencio & Fitzgerald, 2010). Amphibian assemblages on low elevation neo-tropical sites are known to have greater inter-site similarity than those over 700 m (Laurencio & Fitzgerald, 2010). Evidence to support this in the NWG comes from novel, point endemic, amphibian species being described from sites at either end of the study area (Biju et al. 2009; Padhye, 2013). Further evidence comes from plateau specialist reptiles (Chikane, 2012) and novel plateau specialists (Mirza et al. 2014). Where plateau connectivity is good assemblages can be maintained by immigration as in the low lying coastal areas species richness is likely to be higher than on the topographically isolated high-level sites (Stevens, 1992).

Anthropogenic disturbance negatively impacts amphibians (Nogues-Bravo et al. 2008). It changes species dominance and produces a more homogenised assemblage (Cortés-Gómez, Castro-Herrera & Urbina-Cardona, 2013). Less mobile species with lower reproductive rates and those with specific habitat and dietary requirements are most vulnerable (Newbold et al. 2014). In the worst affected habitats species richness may be reduced by 76.5% and abundance by 39.5% (Newbold et al. 2015). Activity that changes soil characteristics has an impact on amphibians (Cortés-Gómez, Castro-Herrera & Urbina-Cardona, 2013) in the context of cultivation it reduces diversity (Gardner, Barlow & Peres,

2007) and in paddy specifically amphibians are negatively impacted (Tsuji et al. 2011). With the majority (61%) of southern WG species only found on undisturbed sites (Krishnamurthy, 2003).

Amphibians make excellent surrogate taxa in richness-hotspot studies as they are highly susceptible to both aquatic and terrestrial environmental changes resulting from their permeable skin and biphasic life history (Hopkins, 2007; Lewandowski, Noss & Parsons, 2010). Additionally, they are sensitive to anthropogenic land-use changes as they rapidly bio-accumulate pollutants (Hopkins, 2007). Restricted range species are the most effective in capturing levels of endemism and endangered species (Trindade-Filho & Loyola, 2011).

Given that the amphibians of the NWG are part of a data deficient, globally threatened group and the NWG is a key conservation priority it is highly important that the gap in their ecological data is urgently addressed. There is urgency for this information as these rare fragile ecosystems are being rapidly lost or degraded by human activity (Biju et al. 2009; Aravind & Gururaja, 2011; Giri, 2016). This study will conduct the first quantitative comparative study of the amphibian fauna specific to the rocky plateaus in the NWG and the coastal lowlands together with their abiotic distribution drivers (Beier et al. 2015). The results will provide a baseline to assist in forming evidence-based conservation decisions (Humraskar & Velho, 2007; Aravind & Gururaja, 2011; Sutherland & Wordley 2017).

The study will seek to answer the simple questions:

- How do the western Maharashtan rocky plateau amphibian assemblages differ?
- If they differ ‘what are the environmental factors driving the distribution pattern?
- Then within patterns derived from the environment ‘how do anthropogenic land-uses change amphibian distribution?

It will compare assemblages across a range of spatial scales. Given the global importance of rocky plateaus such studies provide valuable baseline data and information for their conservation in many

regions of the globe and in general on island-like terrestrial habitat patches (Adams et al. 2013; Sutherland et al. 2017).

3.2 Methods

3.2.1 Study area

The WG are a 1600km long chain of hills running north-south parallel to, and around 35km inland from, the south west coast of India from approximately 8°N to 21°N (Fig 1.0-1 & 4). Geological and macroclimatic differences compound the physical barriers created by the escarpment along the western edge of the WG and the two breaks in the hills, resulting in three distinct eco-regions, Southern, Central and NWG (Fig. 1.0.1 [Bossuyt et al. 2004; Vidya et al. 2005; Ram et al. 2015; IMD, 2016]). The NWG are distinct being formed from the Cretaceous basalt outpourings that form the Deccan Traps (DT [Widdowson & Cox, 1996; Widdowson, 2010]). Intense chemical weathering has created a landscape of lateritic soils which have in places formed plateaus of lateritic duricrusts or ferricretes (Widdowson, 2007). Erosion has left these plateaus as hilltop carapaces above the escarpment and fragmented, but extensive, plateaus in the Konkan below (Widdowson & Cox, 1996).

Macroclimate varies in study area along elevation and latitudinal clines. Seasonality increases towards the north of the study area which receives some ten days less rain than the southern sites (Davidar, Puyravaud & Leigh Jr, 2005; IMD, 2016). The longevity and continuity of rainfall is particularly important for amphibians (Williams & Hero, 2001). Rainfall is at its maximum on the high-level sites (4-9000mm per annum, PA) peaking on the high-level plateaus in the south of the study area with low level Konkan sites being relatively dry receiving <2000mm PA (Hobbhahn et al. 2006; India, 2017). Temperature and covariable pool physio-chemistry is expected to change with elevation.

3.2.2 Study design

To determine the spatial distribution of individual amphibian species and their distribution abiotic drivers 13 representative lateritic plateaus in western Maharashtra distributed over 2° latitude (15.89°-17.92°N) and a 1112m change in elevation (67-1179m above sea level [m]) were selected (Fig 1.0-2 & 4). For comparative purposes investigative boundaries were established dividing the survey area into two Regions, High and Low separated by the escarpment, and each Region into three Eco-zones (Low South, Low Central; Low North, High South, High Central, High North) to capture latitudinal variation above the scale of site (Fig 1.0-4 [Strayer, et al. 2003])). The 6 Eco-zones may be similar in function to life-zones but in the absence of site specific environmental data for each plateau the term Eco-zone has been applied (Holdridge, 1967). Anthropogenic disturbance type was recorded, and an arbitrary metric calculated by summing the number of disturbance factors observed on each site. The figure is arbitrary but as no relevant literature exists it is considered appropriate for comparative purposes.

3.2.3 Environmental data collection

Macro-environment and microhabitat data were recorded for each site: air, soil and water temperature during survey (°C) and pool pH using a calibrated electrical probe (Hanna Instruments™ HI 9064); pool dissolved oxygen (% saturation) and pool conductivity (µs cm^{-1}) using a calibrated portable meter (YSI Instruments model YSI85-10FT); relative humidity (%RH) and wind speed (mph) using a Protech MS6252B digital relative humidity meter; elevation (m); latitude and longitude for the start and end of each transect using a hand-held GPS (Garmin™ 60csx GPS). Weather during the survey and microhabitats for each transect including presence of soil, pools and streams, maximum loose rock size (mm), number of rocks >50mm and woody plant cover (%) were recorded.

Disturbance factors assessed were: removal of loose rocks, surfaced road, unsurfaced road, built structures on the plateau, domesticated animal grazing, surfaced road within 200m of plateau, tourism,

part conversion to plantation, adjacent built structures, and importation of topsoil (Table 3.0-3). The sites with 0-3 factors were categorised as Light disturbance, 4-7 Medium Disturbance, 8+ High Disturbance. Human activity changed the availability of some classes of microhabitat, most notably the removal of loose rocks, reduction in woody plants in conversion for grazing and agriculture, creation of pools on some low-level sites and importation of soil at Panchgani (Fig 11b).

3.2.4 Field data collection-amphibians

The survey timing was set for the known range of amphibian autecology, encompassing species exhibiting both explosive and prolonged breeding strategies (Daniel, 2002; Wells & Schwartz, 2007).

Detection probability was maximised by performing both diurnal and nocturnal surveys during two temporally comparable survey seasons at the onset of the monsoon rains in late July to early August in 2013 and 2014 (Crump & Scott, 1994).

Visual Encounter Surveys (VES) with refugia searching were performed along 400 x 6 m line transects at each plateau (Crump & Scott, 1994; Doan, 2003; Marsh & Haywood, 2010). Transect locations were determined on each site to sample all available microhabitats. Amphibian identity, abundance together with their microhabitats and environment were recorded for each section of the transect (Babbitt, Veysey & Tanner, 2009). Where certain identity could not be determined in the field photographs were taken to facilitate later clarification. Where a species has been found in multiple habitat types we describe it as a habitat *generalist* (Aravind & Gururaja, 2011; Lewis et al., 2010; Katwate, Apte & Raut, 2013; IUCN, 2016-2; Padhye & Ghate, 2012; Seshadri et al., 2016).

All animals were handled with single use vinyl gloves, measured on site and released back to their original locations recording snout to vent length (SVL) and live wet mass. SVL which was measured with Lousware LSWCL1810 precision dial callipers (± 0.05mm), mass estimated with Pesola™ spring

balances (±0.01g). Caecilians were measured using squeeze-boxes to minimise handling and stress ((Fig 3.0-2 [Quinn & Jones, 1974]).

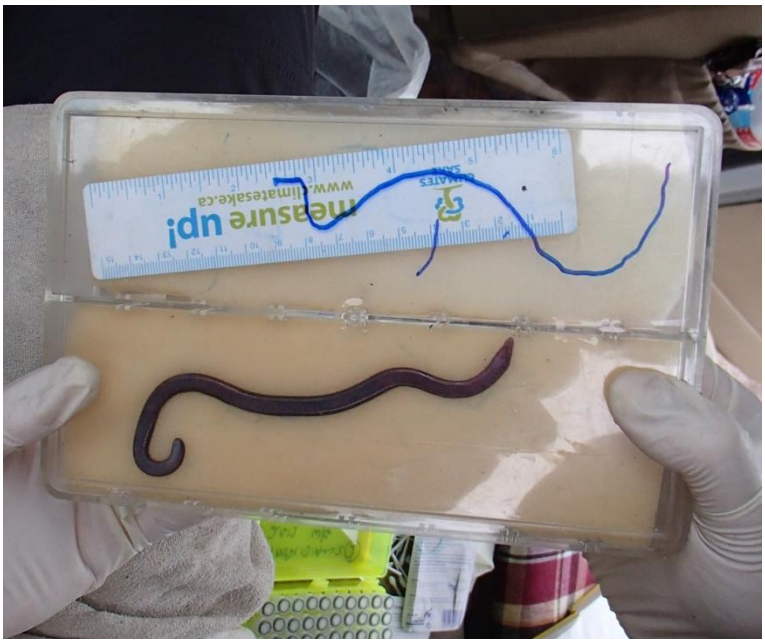


Figure 3.0-2 (2). Details of a squeeze box used to measure caecilians. It is made from a clear plastic box with sterilized foam rubber insert. The animal is placed on the foam, the lid closed and a line drawn along it. The animal can then be released or moved. A piece of string can be placed on the line, lifted off and measured on a rule.

3.2.5 Taxon identification

Taxa were identified using morphological comparison with the most up to date literature available (Bhatta, 1998; Dubois, Ohler & Biju, 2001; Bossuyt, 2002; Daniel, 2002; Giri, Wilkinson & Gower, 2003; Kuramoto & Joshy, 2003; Giri, Gower & Wilkinson, 2004; Gurushankara, Krishnamurthy & Vasudev, 2007; Kuramoto et al., 2007; Biju et al., 2009; Padhye, 2013; Padhye 2014; Dinesh et al., 2015; Frost, 2015; Dahanukar et al., 2016; Dinesh et al., 2017; Garg & Biju, 2016; Garg & Biju, 2017). However, some genera within the area are taxonomically cryptic or unstable, for example the *Fejervarya-Zakerana* and *Indirana* complexes (Dahanukar et al., 2016; Garg & Biju, 2016; Garg & Biju, 2017). In cases where species-level identification may be in doubt we use ‘cf’. Species will be used in the text even when it may refer to a putative species or genera.

3.2.6 Data analysis

Spatial autocorrelation in environmental and biotic data was first assessed by comparing Bray-Curtis similarity and Euclidian distance matrices with an inter-site distance matrix using the RELATE routine with 999 randomised permutations (Legendre, 1993; Legendre et al., 2002).

The impact of latitude, elevation, climate, land-use, disturbance intensity and microhabitat availability were assessed for impact on amphibian species distribution and abundance in each of the spatial sub-units. Land-use was related to community profile including the percentage of generalist or disturbance intolerant species.

Environmental correlations with the spatial sub-units were assessed with either Pearson Product Moment or Spearman Rank Correlations in Minitab™ v17 before their spatial relationships were assessed by non-metric multi-dimensional scaling ordination (nmMDS) of Euclidian Distance matrices of normalised data (Kent, 2012; Clarke & Gorley, 2015).

Macroscale analysis of amphibian distribution used a series of Permutational Manova tests performed on Bray-Curtis square root transformed data for the individual elements of year, Region, Eco-zone, latitude and elevation as well as nestedness using combinations of site, year, latitude and elevation in Permanova+, Primer-e v7 (Jolliffe, 2002; Anderson et al. 2008; Clarke, 2015).

Detailed pattern analyses were performed for a range of richness and diversity indices: species abundance, alpha diversity, Shannon-Weiner (H') and Inverse Simpson's (1-D) indices and Pielou's (J) community evenness index. These were correlated with elevation, latitude and microhabitats in Minitab™ v17. Spatial turnover, as measured via Whittaker's Beta diversity (b_w), was examined using

Whittaker's formulae: ($b_w = \frac{S}{\overline{a}}$) where S = total types in the Region and $\overline{a}$ the average site sample species diversity, calculated in the PAST software (Whittaker, 1960; Hammer, Harper & Ryan, 2001).

The environmental variables, including disturbance, that explained amphibian distribution were determined for all the taxa and for individual families (BEST routine in Primer-e v7). This routine determines the extent of matrix correlation between the Bray-Curtis similarity matrix and a Euclidian distance matrix for environmental variables, selecting a subset of variables with the greatest correlation. The key individual species in generating spatial structure were identified using LINKTREE clustering methodology in Primer e v7 (Clarke & Gorley, 2015).

Unless stated otherwise all statistical analyses were conducted in Primer-e v7 (Primer-e Ltd., Plymouth, UK).

3.3 Results

3.3.1 Spatial structuring in the environment

Pool environmental data were not significantly spatially auto-correlated (RELATE; ρ=0.177, P=0.0 7). Temperature declined with increasing elevation but not latitude. Water conductivity increased with both elevation and latitude (Table 3.0-1 & 2). Except for Pond Presence, which declined with elevation, the other physio-chemical and habitat variables increased with elevation but showed no relationship with latitude (Table 3.0-2). Rainfall frequency was 12.7 greater on High Region sites.

Table 3.0-1. Physio-chemical parameters with separate data for each Region. Temperature (°C), water conductivity (µs cm^{-1}).

Variable	Region	Mean	SE Mean	Minimum	Maximum
Water T	Low	30.9	0.4	26.2	36.4
Water T	High	22.5	0.2	19.3	28.3
Water T	All	24.8	0.3	19.3	36.1
pH	Low	6.7	0.1	4.9	9.6
pH	High	7.6	0.2	5.3	12.2

pH	All	7.3	0.1	5.0	12.2
Conductivity	Low	37.1	1.6	16.4	63.9
Conductivity	High	24.1	1.2	2	56.1
Conductivity	All	30.8	1.2	2	63.9

Table 3.0-2. Spearman Rank Correlations with physio-chemical and habitat factors. P<0.01=**, P<0.05=*. Units used: temperature (°C), conductivity (µs cm^{-1}), wind speed (mph), relative humidity (%RH); woody plant cover and surface water (% of area), pond presence (presence-absence).

Environmental factor	**Elevation ρ**	**Latitude ρ**
Air Temperature	-0.933**	
Conductivity	0.523 (P=0.07)	0.766**
pH	0.244**	
Windspeed	0.598*	
Relative Humidity	0.588*	
Woody Plant Cover	0.704**	
Pond Presence	-0.717**	
Surface water	0.611*	

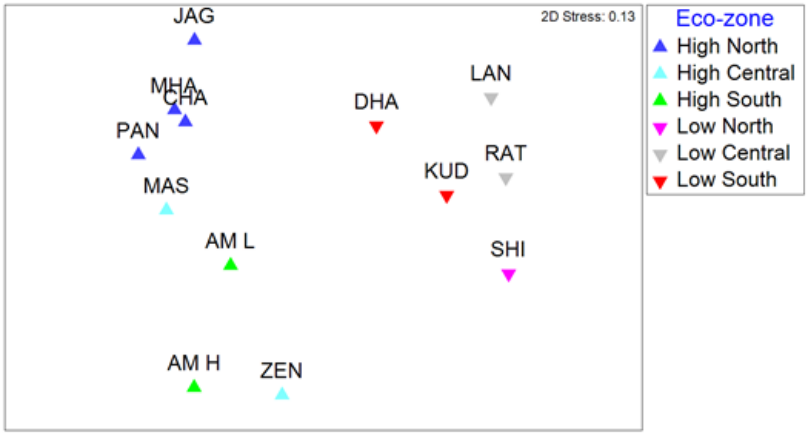


Figure 3.0-3. nmMDS plot of a Euclidian distance matrix of square root transformed and normalised environmental data. Distance between points in the nmMDS plots is relative to the difference in the environmental character. Site codes: ZEN-Zenda; CHA-Chalkewadi; JAG-Jagmin; MHA-Mhavashi; AM l-Amboli Low; AM H-Amboli High; MAS-Masai; RAT-Ratnagiri; DHA-Dhamapur; LAN-Lanja; SHI-Shipole; KUD-Kudopi; PAN-Panchgani.

In the nmMDS ordination the distance between data points is relative to their difference (Fig 3.0-3). The High North clustered in the top left of the plot indicating they are more like each other than the remaining sites; there is overlap between the High South Sites and High Central. The Low Region sites to the top right of the plot and clearly distinct from the High Region sites. The low disturbance

sites of Amboli High and Zenda are close together possibly a result of both retaining much of their loose rock cover (Table 3.0-3).

Table 3.0-3. Site descriptions with land use, elevation in m above sea level, land-use, disturbance Intensity and Eco-zone.

Site	Latitude	Longitude	Land use	Disturbance intensity	Eco-zone
Chalkewadi	17.5736	73.8261	Wind turbine	Medium	High North
Jagmin	17.5927	73.8181	Light	Light	High North
Mhavashi	17.4310	73.9313	Wind turbine	Medium	High North
Panchgani	17.9217	73.8045	Tourism	High	High North
Masai	16.8181	74.0779	Tourism	High	High Central
Zenda	16.9226	73.8072	Light	Light	High Central
Amboli Low	15.9374	74.0027	Tourism	High	High South
Amboli High	15.8903	74.0403	Light	Light	High South
Shipole	17.9735	73.0527	Agriculture	Light	Low North
Ratnagiri	16.9627	73.2962	Agriculture	Medium	Low Central
Lanja	16.7419	73.4204	Light	Light	Low Central
Kudopi	16.2327	73.5105	Natural grazing	Light	Low South
Dhamapur	16.0315	73.584	Agriculture	Medium	Low South

3.3.2 Distribution patterns in the biota

Differences in amphibian assemblages, endemism, abundance, alpha, beta and gamma diversity are detectable at most spatial scales. Pool biotic data were not significantly spatially auto-correlated (RELATE; $\rho = -0.007$, $P = 0.5$).

A total of 325 amphibians were detected representing 2 orders, 6 families and 21 species (Table A.2.1 & 2). Only plateaus that were safe to access were surveyed at night so only the 276 individuals found in diurnal surveys were included in the analysis. Mean site abundance did not vary between Regions but High Region sites were more variable (Table 3.0-4). Southern sites had higher mean abundance then either central or northern sites (Table 3.0-4). Gamma diversity was similar in each Region (High

10, Low 11) but each contained different species (Table A.2.2). Most species being found either above (8) or below (9) the escarpment only 2 species were found in both Regions. Distribution was more spatially restricted above the escarpment, with 7 taxa found only in a single Eco-zone above the escarpment compared to 3 below. There were 3 idiosyncratic taxa in the Low Region and 4 in the High Region - i.e. taxa found at a single site (Table A.2.2). Mean site alpha diversity was much higher in the Low Region (5.2) than above the escarpment (2.88), there was no latitudinal signal (Table 3.5). Eco-zone alpha diversity, number of species, was highest in Low Central and South Eco-zones 9 species in each plus the *Fejervarya* complex (App. 2, Table 2). Mean site alpha diversity in each High Region Eco-zone (2.75) was less than that of the Low Region Eco-zones (7.33). High Region beta diversity (b_w) was greater than in the Low Region (3.52, 1.88 respectively; Table 3.5). High Region β_w increased significantly with latitude, elevation increased with latitude ($R^2 = 0.99$, $F_{(1,2)} = 115.31$, $p = 0.06$). Below the escarpment there was a non-significant increase in β_w ($p = 0.8$). The High North Eco-zone had the highest β_w value (1.465), it also has more land-use types (3) than other Eco-zones, greater variation in topography and higher rainfall seasonality there was no significant impact on alpha diversity (Table 3.0-4). The lowest β_w values were for southern Eco-zones where both Low South and High South Eco-zones had the same values (Table 3.0-5).

The IUCN Red List describes 1 sample species as critically endangered, 1 endangered, 4 data deficient and 2 awaiting listing, 11 were endemic to India or the WG and an additional 2 endemic to Asia (Table A.2.2 & 3) Twice as many Indian/WG endemics were found in the High Region (8) than in the Low (4) and the 2 Asian endemics were only found in the Low Region. Despite being classified as endangered *Fejervarya* (*Minervarya) sahyadris* was found on all low sites (Table A.2.2 [IUCN, 2016-2]). The most abundant species, *Xanthophryne tigerina*, is classified as critically endangered (IUCN, 2016-2).

Table 3.0-4. Comparisons of mean site abundance, alpha, beta (b_w) diversities and Shannon-Wiener Index (H') by Area, Region and Eco-zone. N = Mean Site Abundance; Low North single site = *; SD = 1 x Standard Deviation.

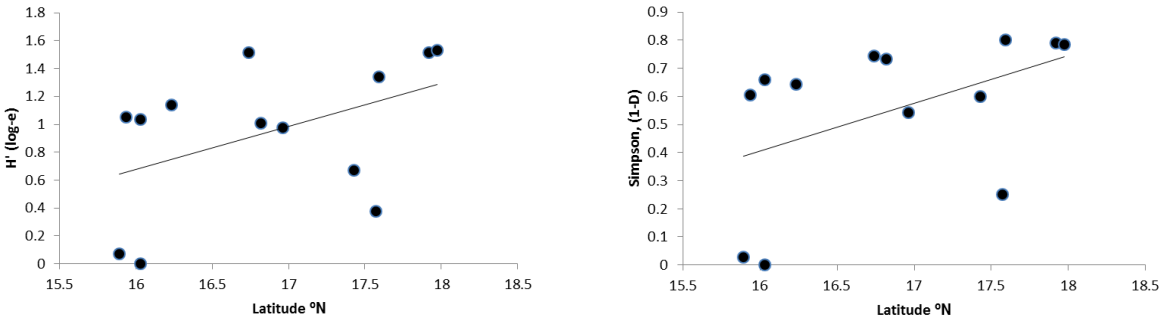
Eco-zone	Mean Site N (SD)	Alpha Diversity	Beta Diversity	H'
Area	21.23 (18.67)	3.76 (1.92)		
High Region	21.57 (24.05	2.88 (1.36)	3.52	0.76 (0.57)
Low Region	20.83 (11.94)	5.2 (1.92)	1.88	1.24 (0.32)
High North	12 (8.37)	3.25	1.46	
High Central	4.5 (2.12)	2	1	
High South	48.5 (34.6)	3	0.67	
Low North	18 (*)	6	1	
Low Central	21 (4.24)	6	0.75	
Low South	31 (12.73)	4	0.67	

Species diversity and dominance increased with Latitude (Fig 3.3a & b). At inter-region scale, there were differences in diversity both Shannon H' and b_w with the High Region having the lower values (Table 3.4). Community evenness (J) did not vary between Regions and none of the other indices examined for site data were correlated with elevation or latitude (maxim R = 0.8; minimum P = 0.1.

Site alpha diversity, Shannon-Weiner Diversity (H') and Pielou's community evenness indices were correlated to a number of abiotic variables (Table 3.5).

Table 3.0-5. Assemblage relationships with the environmental variables. Alpha Diversity is the number of species present; H' is Shannon-Wiener species richness and J is Pielou's community evenness index. Spearman Rank Correlations P<0.05 unless stated otherwise.

Abiotic Element	Alpha Diversity	H'	J'
Wind Speed	-0.641	-0.532, P=0.06	
Air temperature	0.532, P=0.06		
Rainfall frequency	-0.536		
Maximum loose rock size			-0.567
Number of rocks >50mm			-0.559
Presence of ponds	0.639		



a) *b)*

Figure 3.0-4 a & b. a) Shannon_Weiner, H' diversity plotted against Latitude, ρ=0.485, p<0.05. b) Inverse Simpson Domminance Index, 1-D, plotted against Latitude, ρ=0.569, p<0.05.

3.3.3 Macroscale patterns

Only PC1 of the 2 component PCA of environmental data was found to be significant in the first Permanova and carried forwards to further analysis it explained 36.2% of variation. Permanova Components of Variation (Table 3.0-6) found sites were most dissimilar at the largest spatial scale, that of Region (38%). Elevation explained twice as much difference in site assemblages as latitude (24 & 12% respectively). The first axis of the Environment PCA had the same explanatory power as latitude (12%) but half that of Elevation (24%) despite 8 of the 15 abiotic variables being correlated with it (Tables 3.5 & 3.6). The amphibian assemblages of each year were similar to one another (P>0.05).

Table 3.0-6. Permanova results for the macroscale factors structuring water beetle distribution. For Environment the eigenvalues from PC1 of a PCA of all habitat and environment variables was used as a covariable in the Permanova. Region refers to the two Regions split by the escarpment, Latitude Grouped is the area divided into three North, Central and South. Elevation refers to the height above sea level for the individual plateaus in the series of Permutational Manova's, (Permanova+, Primer-e). Both the F and P values were calculated from Monte Carlo permutation tests. The square root of the estimate of component of variation is expressed as a % and annotated C of V.

Element	Pseudo F	P (perm)	C of V
Environment PCA	5.4685	<0.05	12
Eco-zone	1.7553	0.1	14
Latitude Group	2.3347	0.1	12
Elevation Group	2.4136	0.06	24
Region	3.0295	0.08	38

The data points in the biotic nmMDS plot do not follow the environmental nmMDS except they both support inter-regional differences with greater heterogeneity in the High Region. Low Region sites data points were more tightly clustered than the environment alone would suggest whilst High Region sites more diverse (Fig. 3.4 & 3.5). Zenda was excluded as it was an outlier that skewed the plot despite being environmentally similar to Amboli High (Fig. 3.4 & 3.5). It is the site with lowest anthropogenic disturbance and the only site with the disturbance intolerant species *Indirana* cf. *chiravesi* (App. 2 Table 1 & 2). Masai (High Central Eco-zone) was environmentally similar to the adjacent High North sites was biotically very different as the only site with *Indotyphlus* cf. *battersbyi* present and the only High Region site with *Sphaerotheca dobsonii*. Mhavashi environmentally similar to its neighbouring High North sites but biotically very different as the only High Region site with more than one *Fejervarya* sp.

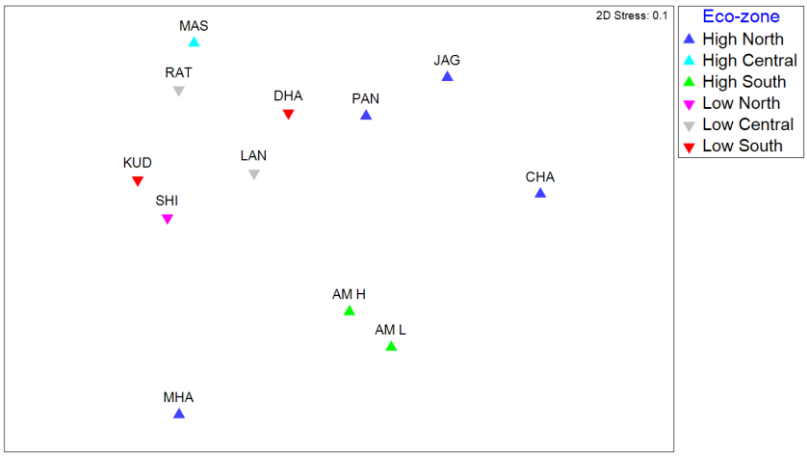


Figure 3.0-5. nmMDS ordination plot of a Bray-Curtis similarity matrix of square root transformed amphibian abundance data, excluding Zenda which as an outlier that skewed the plot. Site codes: CHA-Chalkewadi; JAG-Jagmin; MHA-Mhavashi; AM l-Amboli Low; AM H-Amboli High; MAS-Masai; RAT-Ratnagiri; DHA-Dhamapur; LAN-Lanja; SHI-Shipole; KUD-Kudopi; PAN-Panchgani.

To investigate species driving inter-site relationships a clustering ordination was performed in the LINKTREE routine (Fig 3.0-6; Table 3.0-7). The amphibian assemblages on the Low Region sites are more closely related to each other than any High Region site. The High Region sites are more widely separated from each other and the Low Region at a mean separation of 73% compared to the Low Region inter-site separation of 18%. This supports there being two idiosyncratic sites, both low disturbance sites (Zenda and Amboli High). Each has an amphibian population characterised by

disturbance intolerant (*Indirana* cf. *chiravesi*) or plateau specialist species (*Xanthophryne tigerina*). Two other High Region sites are paired but widely separated from all other sites (Masai and Panchgani). These are spatially distanced but share the same land-use (tourism). Their assemblages, though dominated by generalist species, contain different possibly specialist taxa. Masai has the caecilian *Indotyphlus* cf. *battersbyi* and Panchgani *Fejervarya* (*Zakerana*) cf. *brevipalmata* and *Raorchestes* cf. g*hatei*. The first two are listed by the IUCN Red List as Data Deficient and the third is not assessed. Adjacent sites Chalkewadi (Wind Turbines) and light disturbance Jagmin are closely related suggesting the lack of topographic barriers between sites is more important than land-use in determining amphibian assemblages. The two other High Region sites with differing land-uses (Mhavashi and Amboli Low), wind turbines and tourism, were more similar than their geographic neighbours. Land-use would appear to have a greater impact on amphibian species distribution than spatial factors such as climate and topography.

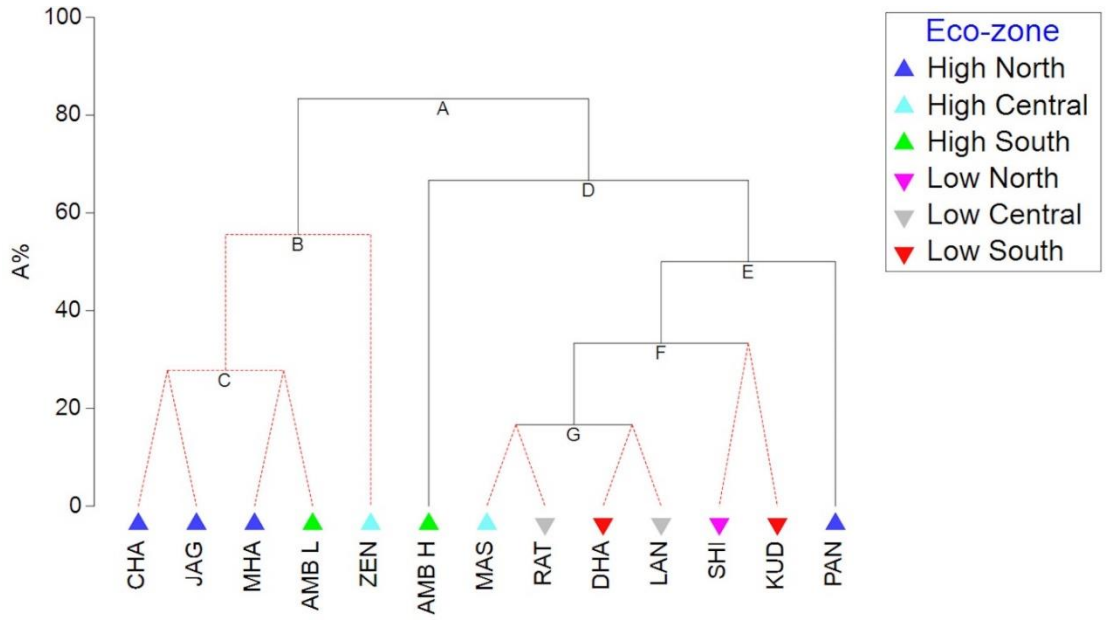


Figure 3.0-6. A clustering ordination in a LINKTREE (Primer-e) analysis of square root transformed species abundance data in a Bray-Curtis similarity matrix. Dashed lines indicate groups not separated (at P<0.05) by Simprof. Site codes: ZEN-Zenda; CHA-Chalkewadi; JAG-Jagmin; MHA-Mhavashi; AM l-Amboli Low; AM H-Amboli High; MAS-Masai; RAT-Ratnagiri; DHA-Dhamapur; LAN-Lanja; SHI-Shipole; KUD-Kudopi; PAN-Panchgani.

Table 3.0-7. Species driving the LINKTREE dendrogram (Fig 3.0-5).

Species	ANOSIM (R) for linkage	% Separation
Hoplobatrachus tigerinus	A: R=0.64	88
Indirana cf. chiravesi	B: R=0.67	103
Fejevarya cf. caperata	C: R=1.00	78
Xanthophryne tigerina or Hoplobatrachus tigerinus	D: R=1.00	61
Raorchestes ghatei or Duttaphrynus melanostrictus or Euphlyctis cf. cyanophlyctis or Fejervarya cf. brevipalmata	E: R=0.47	32
Fejervarya sahyadris	F: R=0.68	26
Sphaerotheca dobsonii or Fejervarya cf. cepfi or Euphlyctis cf. cyanophlyctis	G: R=1.00	24

The BEST BIO ENV (Primer-e) routine was used to assess the relative explanatory power of individual abiotic elements. The differing microhabitat requirements of Anura and Apoda were investigated through separate analyses. Rainfall frequency, woody plant cover, pond presence and water conductivity explained 48.7% of the variation in assemblage composition, with woody plant cover having the highest explanatory power (34.7%; ρ=0.5, P<0.05). Anura alone resulted in a marginally improved BEST BIO ENV result (ρ=0.534, P<0.01) with woody plant cover still making the greatest individual contribution (37.9%,) with 51.1 % of the assemblage explained by three factors: woody plant cover, pond presence and water conductivity. Caecilian distribution was mostly explained by stream presence (46.7%) with most of the pattern (85%) being explained by three variables: frequency of rainfall, presence of rocks and water pH (ρ0.563, P=0.07). Disturbance intensity did not have a significant explanatory power in the BEST BIO ENV routines and was not correlated with abundance, alpha diversity, species richness or community evenness. However, it was

positively correlated with the percentage of generalist and disturbance tolerant species at sites (ρ=0.664, P<0.05).

3.3.4 Spatial distribution and the impact of land use on generalist amphibians

Tourism has the greatest impact shifting the amphibian assemblage towards generalist species followed by wind turbine installation. Agriculture in Low Region sites has no impact (Table 3.0-8). Low Region sites have more generalist species than High Region sites (Table 3.0-8).

Adjacent site comparisons support the effect being caused by the land-use. With the two Amboli sites; Amboli High, low disturbance, 1.5% generalists and Amboli Low, tourism with 75% generalist taxa. Jagmin, low disturbance, has 50% generalists compared to the adjacent wind turbine site, Chalkewadi, with 100% generalist or disturbance tolerant taxa. Some of the 8-generalist species had restricted spatial distribution: *Duttaphrynus melanostrictus* found exclusively above 800 m and mostly above 1000 m; *Gegeneophis* cf. *ramaswamii* found on one High Region site; *Hoplobatrachus tigerinus* were more common on Low Region sites (100:38%); *Microhyla ornata e*xclusively Low Region. (App. 2, Table 1). Two generalist species, *Uperodon globulosus* and *Polypedates maculatus*, were rare in the sample represented by single specimens on Low Region plateaus (Table A.2.2). The Regions held different percentages of generalist species (Low, 61%; High 51.2%).

Table 3.0-8. Percentage of generalist and disturbance tolerant species on each plateau with land use and summaries by land use class. Some sites did not have all taxa identified and this will be referred to where appropriate in the text. Low Disturbance sites are annotated for Region (LR)-Low Region; (HR)-High Region.

Site	Land Use	% Generalist Species
Chalkewadi	Wind Turbines	100
Panchgani	Tourism	80
Amboli Low	Tourism	75
Masai	Tourism/Agriculture	66.6
Lanja	Light Disturbance (LR)	63
Kudopi	Light Disturbance (LR)	60
Mhavashi	Wind Turbines	50
Jagmin	Light Disturbance	50
Ratnagiri	Agriculture	50
Dhamapur	Agriculture	50
Shipole	Light Disturbance (LR)	33
Zenda	Light Disturbance (HR)	0
Amboli High	Light Disturbance (HR)	1.4
All Sites	Mean	54
Tourism	Mean	87.5
Wind Turbines	Mean	75
Agriculture	Mean	52
Low Disturbance	Mean	50 (LR)
Low Disturbance	Mean	17.3 (HR)

3.3.5 Body size and mass distribution

Anuran body size (SVL) and wet mass were both positively correlated with elevation ($r=0.500$, $P<0.001$; $r=0.221$, $P<0.01$ respectively). They were less strongly correlated with latitude (SVL; $r=0.149$, $P<0.05$; Mass; $r=0.194$, $P<0.01$) possibly reflecting the south to north increase in elevation. Caecilians on their own showed weaker relationships with SVL increasing with latitude ($r=0.4$, $P<0.05$) and with elevation ($r=0.362$, $P=0.06$), no correlation with wet mass.

3.4 Discussion

3.4.1 The biogeography and diversity of amphibians

Amphibian distribution was not spatially random, whilst it followed climatic variables at large spatial scale, isolation, evolutionary history, disturbance from anthropogenic land-use change appears to be more important at a local scale. Environmental changes linked to elevation were the principal factors driving the distribution pattern, but beta diversity and species diversity in Eco-zones increased with latitude. With rainfall frequency, amount of woody plant cover, pond presence and water conductivity being most important but at a family level the drivers varied. The greatest differences were observed at the larger spatial extents i.e. between Regions. Regional abundances were similar, but site abundances were more variable in the High Region. These sites were less diverse and had lower species richness. The amphibians at higher elevations and latitudes were larger and more often endemic. Very widely distributed species were more common in Low Region sites apart from *Duttaphrynus melanostrictus* which was only encountered above 800 m. Those plateaus which had retained high numbers of loose rocks had less even community assemblages dominated by plateau specialist or disturbance intolerant taxa. Anurans were most impacted by the amount of woody plant cover, pond presence and pond water conductivity, with Apoda being affected by rainfall frequency, presence of rocks and pond water pH. Anthropogenic land-use changes the amphibian assemblage composition in respect of the percentage of generalist species. Tourism appears to have had the greatest impact followed by wind-turbine installation and then low intensity agriculture.

3.4.2 Amphibian distribution patterns

The Permanova analysis found elevation had the greatest explanatory power for the amphibian distribution. Its' largest impact was at the inter-region spatial extent. The impact was on the distribution of individual taxa with each Region having similar gamma diversity made up of different taxa, only 2 out of 21 species were found in both Regions. We found 76% of species were high or low

elevation specialists, with our dividing line of 809m, like an Asian meta-analysis which found a dividing line of 838m and a median of ~58% specialist species (Laurance, et al. 2011). They report a greater percentage of lower zone specialists (50:30%) whereas we found the same percentage (38%) of specialists in each zone. Our study supports the findings of Naniwadekar & Vasudevan (2007) who found the proportion of endemics increased with elevation between 700-1300m. We found 8 Indian and WG endemics on high sites and 4 on low, if the criteria are restricted to WG endemics alone the distinction between Regions increases with 6 on high sites and 2 on low (Table A.2.2). Daniels (1992) found the highest number of WG endemics between 800-1000 m and Naniwadekar & Vasudevan (2007) above 700 m, our study, although further north, broadly supports both findings but up to a slightly higher elevation. The study confirms findings from the southern WG that the largest proportion of endemic and unique amphibians was found above 700m (Naniwadekar & Vasudevan, 2007). Low Region connectivity is illustrated by the presence of the Asian endemic generalist species, *Polypedates maculatus* and *Uperodon globulosus,* which were not found in the High Region.

Latitude and elevation do not *per se* regulate amphibian distribution; rather it is the response of specific taxa to changes in the abiotic environment that drives the pattern (Daniels, 1992; Laurance et al. 2011). All the abiotic parameters assessed are known to affect amphibian distribution (Daniels, 1992; Snodgrass et al., 2000; Babbitt, Baber & Tarr, 2003; Naniwadekar & Vasudevan, 2007; Babbitt, Veysey & Tanner, 2009; Gutiérrez-Pesquera et al., 2016). However, the nmMDS pattern of biotic distribution does not fully concur with that of the abiotic. The distribution of the amphibian families in the study area was explained by a small number of abiotic factors identified in the BEST BIO ENV analysis. Three factors explained 51.1% of the anuran distribution: woody plant cover, pond presence and water conductivity. With 85% of the caecilian distribution explained by: frequency of rainfall, presence of rocks and water pH. Of these woody plant cover, pond presence, pH was correlated with elevation and conductivity with elevation and latitude. Rainfall frequency whilst not correlated with elevation or latitude was different at regional scale being 12.7 times greater above the escarpment.

3.4.3 Topography and evolutionary history

In addition to a thermally complex environment the topographical heterogeneity in the WG is known to be an isolating factor (Robin, Sinha & Ramakrishnan, 2010) which can lead to lower regional diversity at higher elevations as seen in this study (Laurencio & Fitzgerald, 2010; Scheffer et al. 2006). LINKTREE analysis supports findings from Costa Rica where sites below 700 m were more similar than those at higher elevation (Laurencio & Fitzgerald, 2010). They go on to describe how this is measurable in beta diversity; again, we support that with higher β_w values above the escarpment when each latitudinal Eco-zone pairs except those in the south of the study area. The distribution pattern observed would support a herpetofauna which is both vicariant and immigrant in origin (Van Bocxlaer, et al. 2006; Van Bocxlaer, et al., 2009). These taxa migrated into the WG after the DT eruptions and were possibly expansion-oriented phenotypes with high adaptive capacity that evolved to adapt to the changing isolation and environment as the DT eroded into isolated rocky plateaus speciating to accommodate the differing environments (Pyron, 2014). Isolation created by the increasing topographical complexity and patchy distribution of rocky plateaus (Widdowson & Cox, 1996; Ghalambor et al. 2006). Our observations reflect this in the High Region with its prominent levels of WG endemics and species with very restricted geographical distribution such as *Xanthophryne tigerina* supplemented by generalist species able to transverse the matrix for example *Duttaphrynus melanostrictus.*

3.4.4 Elevational temperature changes impact amphibian size distribution

Soil temperature is proposed as the best predictor of alpha diversity in southern WG amphibians, however, it was not found to be significant in the NWG in either correlation or the BEST BIO ENV analysis (Naniwadekar & Vasudevan, 2007). However, the decline in abundance, alpha diversity and species richness in most high Eco-zones does reflect the elevational decline in temperature (Rahbek, 1995; Navas, 2002; Watve, 2013). Many amphibians in the NWG display terrestrial behaviour where desiccation is a risk from excessive temperature (Guo & Lu, 2016).

Not only temperature but other factors including wind and relative humidity can lead to desiccation these limit the range of viable sites for specific reproductive modes (Tracy, 1976; da Silva et al. 2012). Relative humidity and wind speed increased with elevation but only wind speed was negatively correlated with both alpha diversity and species richness. BEST BIO ENV identified rainfall and relative humidity as important for three study genera; Philautus sp., Psudophilautus sp. and Raorochestes sp. (Krishnamurthy, Gururaja & Reddy, 2002; Seshadri, Gururaja & Aravind, 2012). They form a recognised risk for other taxa known from lateritic plateaus in the NWG e.g. *Rhacophorus malabaricus* and Indirana sp (Gaitonde & Giri, 2014; Meegaskumbura et al. 2015). The critically endangered *Xanthophryne tigerina* only mates during rain and relies on highly temporary micro pools for egg deposition and for the survival of its' tadpoles which graze terrestrially making two life history stages at risk from breaks in rainfall, low relative humidity and wind (Gaitonde, Giri & Kunte, 2016). Those species with direct development are predominantly found on higher elevation (~1200 m) sites in the southern WG (Naniwadekar & Vasudevan, 2007).

The majority of Anura in the study were collected and associated with terrestrial environments. Guo & Lu (2016) found terrestrial amphibians followed Bergmann's Rule which predicts larger animals will be larger in cooler regions; in the study area we apply this principle to elevation (Bergmann, 1847). Anuran body length and wet mass increased intra-specifically with elevation and a weaker signal in latitude. Caecilians length increased with elevation and latitude, but their wet mass had no relationship. The Caecilian result supports another tropical study which extended to 1050m and found nearly 50% increases in body mass and length (Measey & Van Dongen, 2006). Other studies from the southern WG and in Asia for the genera *Dicroglossidae* observed trends of declining body size with increasing elevation (Naniwadekar & Vasudevan, 2007; Hu et al., 2011). We conclude that the rule appears to apply to some taxa and is related to their behaviour and therefore would only hold only within a clade as originally conceived so the widely held view that there is no overall support for Bergmann's Rule misinterprets the original premise (Adams, 2007).

Water temperature may restrict species distribution in the study area. The Low Region specialists are exposed to a narrower seasonal temperature range (range 25°C, min. 15°C max. 40°C) but a higher study maximum temperature (36.4°C) compared to High Region plateaus (range 38°C, min. 4°C, max. 40°C) with a study maximum of 28.3°C (Watve, 2010). These are beyond recorded critical temperature maximums, both lower, CT_{min} (7.9-8.9°C) and upper CT_{max} (35.4°C), for tropical amphibians (Frishkoff, Hadly & Daily, 2015) and close to those for (sub)tropical amphibians CT_{max} 38.9-42.5°C (Duarte, et al. 2012). For example, *Rhacophorus malabaricus* a WG endemic found between 300-1200 m has a CT_{max} of 34°C (Daniels, 1991). Behavioural mechanisms, including thermal refugia and aestivation, may enable species persistence on the plateaus outside their thermal envelope (Navas, 2006; Duarte et al. 2012). Thermal niche or envelope is proposed as the best predictor for species presence with individual species having an evolved temperature range with warm adapted species having an advantage in anthropogenic landscapes (Frishkoff, Hadly & Daily, 2015). Sub-tropical species have very low warming tolerance and Low Region specialists may therefore be at risk from the predicted temperature increase under climate change models (Duarte et al. 2012; IPCC, 2014; Cunningham et al. 2016).

3.4.5 Spatial distribution of microhabitats influences amphibian distribution

The BEST BIO ENV analysis found ponds to be highly important for anuran distribution in addition to being correlated with amphibian species richness; they were more common below the escarpment. Lentic systems are known to be important for three of the Low Region specialists: *Microhyla ornata*; *Minervarya sahyadris* and *Polypedates maculatus* Woody plants were more common at higher elevations and were important for the distribution of anurans but not their diversity. Loose rock, both abundance and size, were associated with low community evenness as the remote sites where they are still in abundance have low species richness of plateau specialist species, *Indirana* cf. *chirvesi* on *Zenda* and *Xanthophryne tigerina* on Amboli High (Table 3.0-7; A.2.2). The IUCN describe *I.* cf *beddomii* as disturbance intolerant and we would suggest *X. tigerina* should also be described as at risk from disturbance based on the major difference in abundance between the two Amboli sites in

this study, one with little human activity and many rocks, the other with disturbance and fewer rocks (Table A.2.2 [IUCN, 2016-2]). Loose rocks were important for caecilian distribution in addition to rainfall frequency. Soil moisture is known to be important for the group and is represented in our results by rainfall frequency (Bhatta, 1998). We observed non-significant caecilian associations with streams, most were seen within 50 m. They are an important microhabitat for the group where individuals frequently reside in streamside habitats in the dry months (Bhatta, 1998).

Physiochemical factors are known to be important in explaining the distribution of some amphibians (Beebee, 1983; Wyman, 1988). In the BEST analysis water conductivity offered a partial explanation for Anuran distribution and pH for the Caecilians but as both varied with elevation the association is not clear (Table 3.0-7). Both increased with elevation, low pH is reported to be lethal for some amphibians increasing corticosterone levels (Chambers, 2009). Higher levels of conductivity result in reduced amphibian larval fitness (Chambers, 2011).

3.4.6 Rainfall seasonality drives beta diversity

Beta diversity is an important metric for regional biodiversity in amphibians and is known to be related to rainfall, temperature, sunshine and isolation (Laurencio & Fitzgerald, 2010). Beta diversity, Shannon Diversity and Simpson Dominance Indices increased with latitude but not elevation. It is important to remember that there is a latitudinal increase in elevation, 809-1131 m above the escarpment, but only 85-170 m below it. Study area temperature decreased with elevation and rainfall frequency with elevation at a regional scale neither changed with latitude. However, the study area has around 11% fewer day of rain in the north compared to the south (IMD, 2016) and the High Region is more topographically heterogeneous in the north which may be an isolating factor (Widdowson & Cox, 1996). Rainfall seasonality, relative humidity and isolation are proposed as explanations for the diversity clines (Vasanthi, Singh & Raj, 2014) and amphibian diversity in the WG (da Silva et al. 2012).

3.4.7 Amphibian assemblages under a disturbance regime

Our study supports the view that amphibians are susceptible to anthropogenic land-use changes (Tsuji et al. 2011) and generalist species are best adapted for change (Hamer & McDonnell, 2008). Our study shows anthropogenic disturbance shifts the community towards one dominated by disturbance tolerant and generalist species at an individual site scale. As found in other studies at a regional scale climate structure is more important (Cortés-Gómez, Castro-Herrera & Urbina-Cardona, 2013). Studies in the WG note changes in abundance, diversity richness when from forest assemblages to other land-uses but none examine plateaus, wetland ecosystems or shifts in functional groups but see (Anand et al., 2010; Murali & Raman, 2012; Balaji, Sreekar & Rao, 2014).

Disturbance intensity, as measured on our arbitrary scale, was not identified as a key driver of amphibian assemblages in the BEST BIO ENV analyses but the land-use type has an impact. However, the LINKTREE analysis shows the two most individual sites are the least disturbed ones, Amboli High and Zenda, both have communities dominated by specialist of disturbance intolerant species (Fig 3.0-6; A.2.2). At the other end of the scale tourism appears to cause the greatest change (Table 3.0-6). Highly disturbed tourism site Panchgani has 80% generalist species compared to low disturbance Jagmin which is close and a similar elevation with 50% generalists. Amboli High with almost 1.4% generalists adjacent to Amboli Low with 75% generalists (Table 3.0-6&7). Alpha diversity on both tourist sites was at least double that of the low disturbance Amboli High and species richness highest on Panchgani then Amboli Low but these assemblages were dominated by generalist taxa. The critically endangered high-level plateau specialist *Xanthophryne tigerina* was negatively impacted with the tourist site having a population of 14 compared to the low disturbance total of 72 (Table A.2.2). On sites with wind turbines, Chalkewadi and Mhavashi, 100% of identified species were generalists (Table A.2.2). Agriculture is a disturbance known to affect amphibian community

composition (Murali & Raman, 2012) and all low Region sites have some agricultural related disturbance with no detectable impact on the generalist community content (Table 3.0-8 & A.2.2).

3.5 Conclusion

Plateaus amphibian assemblages are highly individual and become increasingly distinct as elevation and topographical heterogeneity increases. Higher elevation sites contained a greater proportion of Indian and Western Ghats endemic species than the lower elevation sites. Macroscale patterns are structured by abiotic changes related to elevation and latitude. Critically endangered and endangered amphibians were found in the Western Ghats and in the Konkan below the escarpment. Anthropogenic land-use changes negatively impacted the amphibian communities by allowing space for a greater proportion of generalist and disturbance tolerant species. That effect was greatest on sites with tourism. The distribution was best described as a pattern in individual species. Whilst there were large scale differences in some diversity measures between sites above and below the escarpment general clines with elevation or latitude were not detected but with a few exceptions: The elevational thermal gradient is enough to support a Bergmann Cline in body length and wet mass in both Anura and Caecilians; Beta diversity was the best diversity measure finding maximum diversity in the north and on high elevation northern sites in particular, supported by a latitudinal increase in both the Shannon Diversity and Inverse Simpson's Dominance Indices. Low disturbance sites above the escarpment are particularly important as they hold communities dominated by either plateau specialists or disturbance intolerant species.

Chapter 4. Micro-habitat distribution drives patch quality for sub-tropical rocky plateau amphibians in the northern Western Ghats, India.

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Author contributions: CJT Designed and implemented the study and authored the paper: TRL assisted with the study design, data collection, taxonomy and editing; DTB assisted with study design; SK assisted and logistics; DP and LD assisted with data collection; DTB assisted with study design, taxonomy and editing; AW assisted with permits and fieldwork; MEK assisted with study design and editing.

Abstract

The importance of patch quality for amphibians is frequently overlooked in distribution models. Here we demonstrate that it is highly important for the persistence of endemic and endangered amphibians found in the threatened and fragile ecosystems that are the rocky plateaus in Western Maharashtra, India. These plateaus are ferricretes of laterite and characterise the northern section of the Western Ghats/Sri Lanka Biodiversity Hotspot, the eighth most important global hotspot and one of the three most threatened by population growth. We present statistically supported habitat associations for endangered and data-deficient Indian amphibians, demonstrating significant relationships between individual species and their microhabitats. Data were collected during early monsoon across two seasons. Twenty-one amphibian taxa were identified from 14 lateritic plateaus between 67 and 1179m above sea level. Twelve of the study taxa had significant associations with microhabitats using a stepwise analysis of the AICc subroutine (distLM, Primer-e, v7). Generalist taxa were associated with

increased numbers of microhabitat types. Non-significant associations are reported for the remaining 9 taxa. Microhabitat distribution was spatially structured and driven by climate and human activity. Woody plants were associated with 44% of high-elevation taxa. Of the 8 low-elevation taxa 63% related to water bodies and 60% of those were associated with pools. Rock size and abundance were important for 33% of high elevation specialists. Three of the 4 caecilians were associated with rocks in addition to soil and stream presence. We conclude the plateaus are individualistic patches whose habitat quality is defined by their microhabitats within climatic zones.

4.1 Introduction

The Western Ghats-Sri Lanka Biodiversity hotspot is the eighth hottest global biodiversity hotspot and one of the three most threatened by human population growth (Cincotta, Wisnewski & Engelman, 2000; Myers et al. 2000; Sloan et al. 2014). The northern section of the Western Ghats (NWG) is unique, being geologically distinct and biologically isolated from the central and southern sections of the Western Ghats (WG) on the Indian peninsular (Fig 1.0-1&3 [Widdowson & Cox 1996; Vidya et al; 2005; Biju et al. 2009; Ram et al. 2015]). Its' rich amphibian fauna contains many critically endangered, endangered species and data deficient species (Padhye & Ghate, 2002; Porembski & Watve, 2005). The area is characterised by rocky flat mesa-like hilltop 'plateaus' formed from ferricretes of laterite, a rock like material with a high metal content (Fig 1.0-2,3&4; Fig 4.0-1 [Porembski & Watve 2005; Watve, 2013; Thorpe & Watve, 2016]). The individual 'plateau' habitat is a complex matrix of microhabitats. The availability of each microhabitat varies between plateaus, but some macroscale patterns are evident. The plateaus are set within a landscape of varying complexity (Lekhak & Yadav, 2012; Thorpe & Watve, 2016). Rocky plateaus are of international importance for their substantial contribution to regional biodiversity and endemism (Pinder et al. 2000; Jocqué et al. 2010; Porembski et al. 2016) and are globally threatened ecosystems (Hopper et al. 2015; Poermbski et al. 2016). Those in the NWG are recognised as threatened and vulnerable ecosystems (Bharucha, 2010).

The WG is home to 161 of India's 419 amphibians in only 5% of its land area, making the WG the most amphibian rich land area in India (Myers et al. 2000; Aravind & Gururaja, 2011; Giri, 2016; Dinesh et al. 2017). In the WG they are a highly diverse group displaying exceptional levels of endemism (87% [Cincotta, Wisnewski & Engelman, 2000; Myers et al. 2000; Giri, 2016]). Many are endemic with a very localised distribution resulting from their Gondwanan vicariant origin, having speciated *in situ* because of topographical isolation and diverse ecological pressures (Ghalambor et al. 2006; Van Bocxlaer et al. 2006; Van Bocxlaer et al 2009; Pyron, 2014; Giri, 2016). The resolution of their taxonomy is improving but in common with much of the palaeo tropics little has been published on their ecology including their habitat requirements and the environmental factors regulating their distribution (but see: Hiragond et al. 2001; Humraskar & Velho, 2007; Aravind & Gururaja, 2011; Raj et al. 2011).

Amphibian distribution is known to be highly dependent upon habitat features (see e.g. Santos-Barrera & Urbina-Cardona, 2011; Balaji, Sreekar & Rao, 2014), resulting in their populations being spatially determined by microhabitat availability. In tropical regions the diversity of specialist micro-environments facilitates elevated levels of species richness and endemism through heterogeneity in: seasonality or microclimate (Wells & Schwartz, 2007), gradients in precipitation (Duellman, 1988; Lee, 1993), soil moisture (Friend & Cellier, 1990; Vonesh, 1998), and elevation (Lynch & Duellman, 1980; Fauth, Crother & Slowinski, 1989). Evidence for this in the WG comes from the high number of reproductive strategies with at least 40 different reproductive strategies currently recognised in the region (Krishnamurthy, Manjunantha & Gururaja, 2001; Haddad & Prado 2005; da Silva et al. 2012; Seshadri, Gururaja & Aravind 2012; Iskandar, Evans & McGuire 2015; Gaitonde, Giri & Kunte, 2016), each using different habitat resources for mate advertising, mating, egg deposition, spawning, tadpole and neonate feeding. In addition to their dependence on specific microhabitats the amphibians of the WG are threatened by the fungal pathogen *Batrachochytrium dendrobatidis* (Molur et al. 2015). To mitigate these risks, networks of suitable sites with adequate connectivity are necessary (Heard et al. 2017).

There is a globally recognised shortfall in amphibian population and ecological data (Gascon, 2005). To address this, the Amphibian Conservation Action Plan (ACAP) was devised by the International Union for the Conservation of Nature (IUCN) in 2005 to prioritise research directions (Gascon, 2005). Two of the four key strategies of ACAP are to understand the causes of population declines and changes in diversity (Gascon, 2005). To achieve this, baseline data are required on their ecological requirements (Williams & Hero, 2001; Amstrup & McDonald, 2010). Specifically, it is highlighted as essential to identify the key environmental and habitat resources required by each taxon (Ernst & Rödel, 2006; Laurance et al. 2011; Menin, Waldez & Lima, 2011). The IUCN recognise the importance of preserving habitat to conserve species (Baillie, Hilton-Taylor & Stuart, 2004). However, the IUCN do not adequately account for habitat specificity in heterogeneous topography, resulting in the ranges of many species being overstated (Ramesh et al. 2017). At present it is almost impossible to assess the conservation status of the amphibians of the WG due to a serious deficiency in ecological data. It is likely WG amphibians reflect the global pattern where the group is declining because of one or more stressors which frequently work synergistically: climate change; habitat destruction; pollution; over-harvesting; alien species introduction and/or disease (Stuart et al. 2004; Young et al. 2005; Hussain, 2012). Further work is urgently needed in the WG in the face of climate change scenarios and alterations in land use (Feeley, Stroud & Perez, 2016).

Amphibian patch occupancy is dependent upon patch quality and regional factors including patch distribution, the nature of the intervening landscape, and climate (Deans & Chalcraft, 2016). The importance of patch quality in regulating species distribution is becoming widely recognised as a key factor (Mortelliti, Amori & Boitani, 2010). Many species distribution studies only consider landscape scale processes as climate suitability when even with a suitable climate species may be excluded by smaller scale processes including microhabitat availability (Ficetola & Bernardi, 2004; Mortelliti, Amori & Boitani, 2010). We propose the availability of a suitable suite of microhabitats on a plateau define its quality and are a result of variations in macroclimate, edaphic processes and anthropogenic activities (Thorpe & Watve, 2016)

Figure 4.0-1. Illustrations of the varied microhabitats present on the lateritic plateaus of western Maharashtra, NWG.

Given that the NWG are part of a key priority for conservation, and that their amphibians are part of a data deficient globally vulnerable group, it is imperative that this shortfall in ecological data is urgently addressed. That urgency is acute for the NWG rocky plateaus, as these fragile ecosystems are being rapidly lost and damaged by human activity and are home to critically endangered endemic species (Biju & Bossuyt, 2009, Aravind & Gururaja, 2011, Giri, 2016). As the first quantitative study of rocky plateau amphibian habitat associations, the data herein will serve as a baseline to help in forming evidence-based conservation decisions (Humraskar & Velho, 2007, Aravind and Gururaja, 2011).

4.2 Materials and Methods

4.2.1 Study area

The study investigated microhabitat associations of individual amphibian taxa on the isolated lateritic plateaus in the NWG (Fig 1.0-3). These island-like plateaus are dominated by areas of exposed rock but contain a varied mixture of other habitats forming a heterogenous mosaic (Fig 4.0-1). The study focussed on 14 representative lateritic plateaus in the areas both above and below the North-South trending escarpment in the northern section of the Western Ghats/Sri Lanka Biodiversity Hotspot in western Maharashtra. The study area extends over 2° latitude (15.89°-17.92°N) and a 1112 m change in plateau elevation (67-1179 m). Above the escarpment the plateaus are raised hilltop carapaces elevated from the ecologically contrasting countryside.

As temperature, rainfall seasonality and rainfall amount vary across the survey area, for comparative purposes the area was sub-divided into 2 Regions (High and Low), separated by the escarpment. Each Region was further subdivided into three arbitrary latitudinal sections: North, Central and South. These are referred to as ‘Eco-zones’ (similar to life-zones but in the absence of specific environmental data for the plateaus the term Eco-zone is preferred (Holdridge, 1967). Rainfall across this area

ranges from <2000 mm per annum on low sites to >6000 mm on high sites peaking at >9000 mm on one high site (Watve, 2010; Watve, 2013; India, 2017).

These sites encompass a range of land-uses (Fig 4.0-1; Table 4.0-1). As anthropogenic disturbance within a patch is likely to change the availability of some microhabitats its type was recorded, and an arbitrary metric calculated by summing the number of disturbance factors observed on each site (Table 4.0-1). Although the figure is arbitrary, no relevant literature exists, and it allows for initial between patch comparisons. Disturbance factors recorded were; removal of loose rocks, surfaced road, unsurfaced road, built structures on the plateau, domesticated animal grazing, surfaced road within 200m of plateau, tourism, part conversion to plantation, adjacent built structures, importation of topsoil. Sites with 0-3 factors were considered to have low levels of disturbance, 4-7 Medium Disturbance, 8+ High Disturbance. Anthropogenic disturbance changed the availability of some classes of microhabitat, most notably the removal of loose rocks, reduction in woody plants in conversion for grazing and agriculture, creation of pools on some low-level sites and importation of soil at Panchgani (Fig 4.0-1).

4.2.2 Field data collection methodology

Sampling of both microhabitat and amphibian presence was performed along the same belt transects concurrently. The rocky plateaus are relatively simple ecosystems dominated by areas of exposed rocks with varying amounts of other microhabitats. Their size varies by an order of magnitude but based upon the smaller sites within the survey it was determined that four belt transects each 100 m long and 6 m wide would adequately encompass all the microhabitat types available on an individual plateau. The direction and path of each transect was determined at each site to maximise sampling of all available microhabitats. The same methodology was applied on each survey on the same plateaus in each year but with different transect locations making a total surveyed area 4800m^2.

To maximise detection, both diurnal and nocturnal surveys were deployed during two temporally comparable survey seasons (Crump & Scott, 1994). Surveying took place each year in the same weeks at the onset of the monsoons in late July to early August in 2013 and 2014 (Crump & Scott, 1994). Survey timing was selected for the known range of amphibian autecology, encompassing taxa with both explosive and prolonged breeding strategies (Daniel, 2002; Wells & Schwatz, 2007).

To make samples comparable, standardised Visual Encounter Surveys (VES) with refugia searching (Crump & Scott, 1994) along the belt transects were performed (Doan, 2003; Vonesh et al. 2010). The identity of each amphibian taxa their abundance and their microhabitat associations were recorded for each section of the transect (Babbitt, Veysey & Tanner, 2009). Where species identity was not immediately obvious in the field photographs were taken to permit later clarification.

Microhabitat variables recorded along the same transects as the VES surveys comprised; maximum refugia rock size (mm), number of loose rocks >50mm, woody plant cover (as % cover on transect), presence of soil depressions with vegetation, presence of flowing streams, presence of static pools, presence of surface flooding (vernal pools). Although some microhabitats co-occurred, e.g. surface flooding and stream presence, all were included in the analysis so that finer scale associations could be detected (Fig 4.0-1). As some NWG amphibians are semi-terrestrial humidity levels may be considered as a micro-habitat therefore Relative humidity included in the analysis, it was measured with a calibrated hygrometer (Hanna Instruments™ HI 9064 [Pounds, Fogden & Campbell, 1999]).

All amphibians were identified using the best available literature, and their nomenclature considered using the latest taxonomical authorities (Bhatta, 1998; Dubois, Ohler & Biju, 2001; Bossuyt, 2002; Giri, Wilkinson & Gower, 2003; Kuromoto & Joshy, 2003; Kuramoto et al. 2007; Biju et al. 2009a; Biju et al. 2009b; Dinesh et al. 2009; Gower et al. 2011; Padhye et al. 2013; Garg et al. 2016; Dinesh et al 2017; Garg et al. 2017). The classification of several of the taxa found in this study is still evolving. While many herpetologists have adopted the new suggested taxonomies entirely, this study adhered to recommendations within (Frost, 2015) and (Smith & Chiszar, 2006) by presenting former

nomenclature alongside more recent identifications to maintain the continuity of identification in years following taxonomic amendments. This system introduces new and unstable taxa with the formerly acknowledged genera first and the newly identified genera in parentheses. For example, although the changes proposed by Frost (2015) for the genus *Rana* were made at the generic level, biologists wishing to recognize the subdivisions of this genus, but maintain the stability of familiar species names and still follow rules of the International Code of Zoological Nomenclature (ICZN), can recognise newly created subdivisions of these genera as subgenera (Smith & Chiszar, 2006; Hillis, 2007; Frost, 2015). Under ICZN rules, the subgenus category may follow the genus name in parentheses, e.g., *Fejervarya* (*Minervarya*) *sahyadris* or *Rana* (*Lithobates*) *pipiens*.

4.2.3 Statistical analytical methods

Primer-e and Permanova+, Primer-e v7 (Anderson, Gorley & Clarke, 2008; Clarke & Gorley, 2015), were used to investigate the relationships between taxa in the study area and their microhabitats. Biotic data were represented by a Bray-Curtis similarity matrix of square root transformed abundance. Environmental data were represented by a Euclidian Distance matrix which was normalised before analysis. Analyses were performed for all taxa combined and each individual taxon. Ordination and visualisation of the model was performed in distance-based redundancy analysis (dbRDA). To identify the microhabitats with significant taxa associations' step-wise analysis was performed in distLM. The step-wise routine commences with a null model then adds each criterion before checking by tentative removal thus optimising the selection. As the sample and number of predictor variables were small the Akaike Information Criterion with second order correction (AICc), was used as it to accounts for the ratio of samples to predictor variables being lower than 40 and performed in distLM (Akaike, 1973; Anderson, Gorley & Clarke, 2008). The explanatory power of microhabitats for the distribution of the biota was assessed using LINKTREE, a form of constrained binary divisive clustering. The routine maximises the value of R at each division in the biotic matrix in concordance with the underlying distribution of microhabitats within each patch (site) with the B% being the difference in each linkage (Clarke & Warwick, 1994; Clarke & Gorley, 2015).

Table 4.0-1. Disturbance values and dominant land use for each site surveyed. To facilitate spatial comment, the study area has been sub divided into three latitudinal zones each side of the escarpment.

Site	Latitude	Longitude	Land use	Disturbance intensity	Eco-zone
Chalkewadi	17.5736	73.8261	Wind turbine	Medium	High North
Jagmin	17.5927	73.8181	Natural grazing	Light	High North
Mhavashi	17.4310	73.9313	Wind turbine	Medium	High North
Panchgani	17.9217	73.8045	Tourism	High	High North
Masai	16.8181	74.0779	Tourism/grazing	High	High Central
Zenda	16.9226	73.8072	Natural grazing	Light	High Central
Amboli Low	15.9374	74.0027	Tourism	High	High South
Amboli High	15.8903	74.0403	Natural grazing	Light	High South
Shipole	17.9735	73.0527	Agriculture	Light	Low North
Ratnagiri	16.9627	73.2962	Agriculture	Medium	Low Central
Lanja	16.7419	73.4204	Natural grazing	Light	Low Central
Kudopi	16.2327	73.5105	Natural grazing	Light	Low South
Dhamapur	16.0315	73.584	Agriculture	Medium	Low South

4.2.4 Ethics statement

Sampling was undertaken by kind permission of the Indian National Biodiversity Authority, Chenai, India under permit number: Maharashtra 2014 MC200621.

The advice from the representative of the University of Plymouth's Animal Welfare and Ethics Committee was that no formal consent was required since the animals were only observed or received minimal handling on their site of origin. We followed strict handling and preventative measures for cross-contamination, following standard practice for working with amphibians as described on http://www.amphibiaweb.org. No endangered animals were specifically targeted in the study.

4.3 Results

A total of 325 individual amphibians from 2 orders, 6 families, and 21 taxa were detected over the two years of study (Table A.2.1 & 2). Abundance, taxa and microhabitats varied between all sites. Only 47% of recorded microhabitat associations were in accordance with the IUCN habitat descriptions (Table 4.0-2 3; IUCN 2016-2). The 21 taxa in the study represent a small proportion of

the known amphibian taxa from India (419 from India [Dinesh et al. 2017] and 161 from Western Ghats [Aravind & Gururaja, 2011]) but almost 40% of those that are known to occur in Maharashtra (Mahabal &Sharma, 2012; Padhye & Ghate, 2012). Distribution data can be accessed in Table A.2.2.

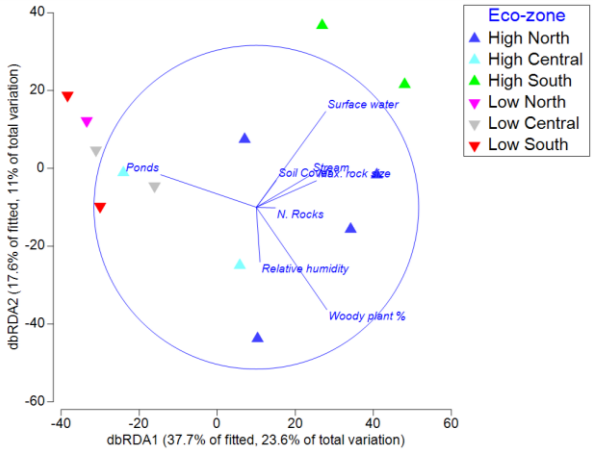

Figure 4.0-2. dbRDA analysis for microhabitats with sites illustrated within Eco-zones to allow spatial comparison. dbRDA1 explained 39.3% of fitted data and 25% of total variation with dbRDA2 explaining 19.3% of fitted data and 12.3% of total variation.

4.3.1 Spatial distribution of microhabitats

Sites could be spatially separated at the macroscale by the relative microhabitat composition with notable differences above and below the escarpment illustrated in Figures 4.0-3 and 4.0-4 (Fig 4.0-2; R=0.53, B%=85%; Fig 3). The two most distinctive sites, Amboli High (Fig 4.0-3; R=0.89, B%=91) and Zenda (Fig 4.0-3; R=0.37, B%=68), are low disturbance sites that have retained much of their loose rock cover and have taxa associated with rock refugia (Fig 3). Lanja, a low disturbance site, is the most charismatic of the Low Region sites (Fig 4.0-3; R=0.55, B%=43; Fig 2). The most diverse Eco-zone was the High North as illustrated by the distribution of the data points in the dbRDA plot, reflecting the impact of three types of land use on microhabitat availability (Fig 4.0-2, Table 4.0-1).

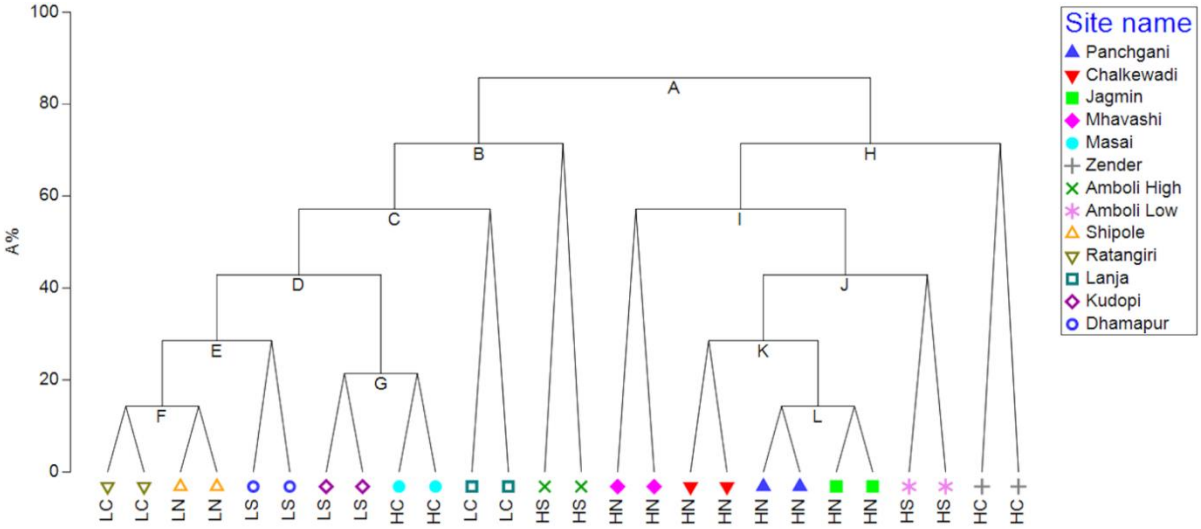

Figure 4.0-3. LINKTREE analysis of plateau similarities based upon microhabitat explanations for the biotic distribution, Primer-e v7. Symbology for individual plateaus for 2 years annotated below for eco-zone, below the escarpment: LN-low north; LC-low central; LS-low south; above the escarpment; HN-high north; HC-high central; HS-high south.

Explanation of LINKTREE annotation:

A: R=0.53; B%=85; Woody plants<-0.117(>-0.0826)

B: R=0.89; B%=91; Max loose rock size<0.832(>2.26) or Surface water<0.848(>1.67) or Woody plants>-0.999(<-1.23)

C: R=0.55; B%=43; Surface water>-1.19(<-1.6) or Woody plants<-0.345(>-0.117)

D: R=0.37; B%=29; Woody plants<-0.738(>-0.607)

E: R=0.54; B%=20; Stream>0.743(<-1.1) or Max loose rock size<-0.871(>0.00354) or Surface water>-0.377(<-0.785) or Woody plants>-0.738(<-0.999)

F: R=0.00; B%=11; Max loose rock size<0.00354(>0.832) or Soil Cover<-0.791(>0) or N. Rocks>-0.0943(<-0.7) or Surface water>-0.785(<-1.19)

G: R=1.00; B%=26; N. Rocks<-1.09(>2.13) or Pools<-0.832(>1.23) or Surface water>0.848(<-1.19) or Soil Cover<0(>1.58) or Max loose rock size<-1.42(>-0.0425) or Stream>0.743(<-0.177) or Woody plants<-0.607(>-0.345)

H: R=0.37; B%=68; N. Rocks<-0.067(>1.63) or Woody plants>0.376(<-0.0826)

I: R=0.54; B%=67; Woody plants>2.31(<1.39) or N. Rocks<-1.03(>-0.997)

J: R=0.63; B%=55; Soil Cover<0(>2.37) or N. Rocks<-0.206(>-0.067)

K: R=0.50; B%=42; Surface water<-0.377(>0.44)

L: R=0.50; B%=23; Stream<-1.1(>1.66) or Max loose rock size<-1.24(>0.786) or Woody plants<0.376(>1.39) or Surface water>1.26(<0.44) or Soil Cover<-0.791(>0) or N. Rocks<-0.997(>-0.206) or Pools<-0.832(>-0.317)

Pools were more abundant below the escarpment where many are manmade; their hydroperiod is shorter on the northern sites and more consistent above the escarpment. The number of annual wet days declines south to north by 11% and there 12.7 times as many wet days above the escarpment (Fig 1.0-3 [IMD 2016; India 2017]). Rainfall amount peaks at Amboli where it exceeds 9000 mm per annum resulting in the microhabitat 'surface water' separating the two Amboli sites from the rest (Fig 4.0-3). Soil is scant on the plateaus but deepens where it has accumulated in shallow depressions in the ferricrete but it has also has been imported onto Panchgani plateau to assist in tourism related activity (Watve, 2013). Loose rock abundance, important as refugia, breeding sites and mate advertising posts, was reduced by collection from accessible sites for construction resulting in a disturbed distribution pattern (Fig 1.0-4; Tables 4.0-2 & 3 [Watve, 2012; Gururaja et al. 2013; Gaitonde & Kunte, 2016; Thorpe & Watve, 2016]). Larger loose rocks were most absent from plateaus below the escarpment and most abundant where human access was difficult for example in the remoter High Region plateaus for example Zenda and Amboli High and to a lesser extent Jagmin. (Fig 4.0-2; Fig 4.0-3 B, H & L [Vonesh, 2001; Krishnamurthy, 2003; Gururaja et al. 2013]). That combined with greater woody plant cover, and for some sites surface water, separated them from the low sites and explained much of the latitudinal divisions (Fig 4.0-2 & 3 A, B, H, I, J, K).

Most sites were characterised by combinations of microhabitats and their associated taxa (Fig 4.0-3; Tables 4.0-2 & 3). Such combinations are key for some taxa for example soil and rocks used by caecilians as refugia and egg deposition sites associated with soil close to water. We found 56% of microhabitats to be impacted by anthropogenic activity Tables 4.0-2 & 3).

4.3.3 Spatial distribution of taxa and explanatory microhabitats

Pond presence on low elevation sites was the most significant abiotic variable separating their amphibian assemblages from those above the escarpment where woody plants, surface water and relative humidity were the principal characters (Fig 4.0-3 & 4). Woody plant abundance, maximum loose rock size, surface water and pond presence were significant factors defining the differences in

the biota above and below the escarpment in both the dbRDA and LINKTREE analyses (Fig 4.0-2; Fig 4.0-3 A, B & D).

High-level sites had 9 taxa not found on low sites (Fig 4.0-2 & 3; Tables 4.0-2 & 3). Woody plants were significantly associated with 44% of exclusive high-level taxa with no such associations for low-level specialists (Tables 2 & 3). Of the 8-taxa found exclusively on low sites 63% had significant relationships with water bodies and 60% of those were associated with pools compared to only 22% on high-level sites. However, all 8 had a relationship with the co-occurring surface flooding, highlighting the need to carefully define the types of water body.

Twelve of the 21-study taxa had significant habitat associations with the remaining 9 having associations that, whilst not significant, were identifiable (Tables 2 & 3). Taxa in the study are described as generalists after the IUCN description where they lack habitat specificity. Generalists that are very widely distributed indicating broad climatic and habitat tolerances are described as ubiquitous (IUCN, 2016-2). The remaining taxon, *Uperodon globulosus*, characterised as a generalist, was only detected when it was raining and had a relationship with relative humidity perhaps explaining its limited detection (Table 3 [IUCN, 2016-2]). The generalist taxa did not have a noticeably higher number of habitat associations than other taxa except *Hoplobatrachus tigerinus*, which whilst currently described as a generalist, should more appropriately be assessed as ubiquitous.

Some 52% taxa were found in habitats other than those recorded by the IUCN, with 91% of the taxa sampled not previously recorded from lateritic plateaus (IUCN, 2016-2). Just over 67% of taxa in the study were associated with water bodies. Surface Flooding was the most important form of water on the plateaus being significant for 48% of taxa, Pools for 33% and Streams for 24%. Of the pool specialists 50% were only found on low level sites where pools were more common. Loose rocks measured by both size and abundance were the next most important microhabitat being significant for 33% of taxa, 19% with small rock abundance and 14% associated with large rocks. Rock sizes and abundance were meaningful in defining the different Regions where large rocks were important for

33% of high-level specialists (Tables 4.0-2 & 3). The abundance of small rocks (<50 mm) was essential for 33% of exclusively low-level taxa but only one high-level specialist (Tables 4.0-2 & 3).

There were 29% of taxa associated with soil-filled depressions. Only 19% of taxa were associated with woody plants despite their being one of the defining microhabitats (Fig 4.0-2, Tables 4.0-2 & 3). The IUCN lists just 2 of the 21 taxa found as being associated with lateritic plateaus (IUCN, 2016-2). Generalist taxa were associated with a higher number of microhabitats (mean 3.7) than the other taxa (1.7). *Fejervarya* (*Zakerana*) cf. *cepfi, Raorchestes* cf. g*hatei* have not been assessed yet and their association should be noted with their first assessment. *Fejervarya* (*Zakerana*) cf. *caperata, Gegeneophis seshachari, Indotyphlus maharashtraensis* and *Indotyphlus* cf. *battersbyi* are all data deficient, thus the data presented here will form part of their initial assessment.

Many amphibians were detected under lateritic rock refugia in diurnal surveys. Only 5 taxa, *Hoplobatrachus tigerinus*, *Fejevarya* cf. *caperata*, *Fejevarya* (*Minevarya*) cf. *sahyadris*, *Indotyplus* cf. *beddomii* and *Xanthophryne tigerina* were found across open areas during the day, and these were only encountered during rainy periods. The above open area taxa were often well camouflaged against the texture of the lateritic rock or among short grass growing on soil depressions. Nocturnal transects confirmed the presence of most of the diurnal anurans without adding new taxa to the sample.

Table 4.0-2. Habitat association results from significant habitat associations identified in step wise analysis using AICc in DistLM, Permanova+, Primer-e v7, where *=P<0.05, **=P<0.01. IUCN threat status and known habitat associations accessed 10/02/2017 (IUCN, 2016-2). NA- Not Assessed; DD-Data Deficient; LC-Least Concern; E-Endangered; CE-Critically Endangered. Population stability:/S-Stable; /D-Decreasing; /I-Increasing.

Species	**IUCN Status**	**Relative humidity**	**Maximum size of loose rocks**	**Abundance of small rocks**	**Woody plant cover**	**Soil area**	**Stream presence**	**Pool presence**	**Surface flooding**	**Habitat concordance**	**Elevation observed**	**Known Habitat Associations (IUCN)**
All taxa combined		**			**			**	**		*0-1179*	
Duttaphrynus melanostrictus	*LC/I*				*		*	*	*0.09*	*x*	*809-1131*	Generalist
Euphlyctis cf. *cyanophlyctis*	*LC/S*						*			*x*	*85-1131*	Lentic, ephemeral water, forest, shrubland
Fejervarya cf. *caperata*	*DD*						*0.07*			*x*	*1156-1090*	Semi-aquatic, grassland, plateaus, disturbance tolerant
Fejervarya cf. *cepfi*	*NA*	*0.08*				*			**		*85-156*	Degraded forest
Gegeneophis cf. *ramaswamii*	*LC/S*					*0.08*				*x*	*809*	Generalist, fossorial.
Gegeneophis seshachari	*DD*			**		*		*	**		*90-156*	Forest, plantations, gardens, degraded forest
Hoplobatrachus tigerinus	*LC/S*	**			**		*	**	*	*x*	*67-1131*	Generalist very adaptable
Indirana cf. *chiravesi*	*LC/D*			*				*		*x*	*1015*	Aquatic, lotic
Indotyphlus maharashtraensis	*DD*		*		*		**			*x*	*1179*	Dry grassland
Microhyla ornata	*LC*			**		*		*	*0.06*	*x*	*85-170*	Savanna, shrubland, grassland, lentic, lotic
Fejervarya sahyadris	*E/D*	*		*				**	**		*85-170*	Grassland, pasture, seasonal flooding, lentic
Xanthophryne tigerina	*CE/D*	*0.08*	**						*	*x*	*809-854*	Lateritic plateaus

Table 4.0-3. The most important microhabitats for taxa that tested without significant habitat associations in the AICc analysis in DistLM Permanova+, Primer-e v7. IUCN threat status and known habitat associations accessed 10/02/2017 (IUCN, 2016-2). NA- Not Assessed; DD-Data Deficient; LC-Least Concern; E-Endangered; CE-Critically Endangered. Population stability:/S-Stable; /D-Decreasing; /I-Increasing.

Species	**IUCN Status**	**Relative humidity**	**Maximum size of loose rocks**	**Abundance of small rocks**	**Woody plant cover**	**Soil area**	**Stream presence**	**Pool presence**	**Surface flooding**	**Habitat concordance**	**Elevation, m**	**Known Habitat Associations (IUCN)**
Fejervarya cf. *brevipalmata*	*DD*					*x*			*x*	*x*	*1131-*	Forest, grassland, wetland, degraded forest
Fejervarya sp.					*x*						*1090*	
Indotyphlus cf. *battersbyi*	*DD*		*x*								*974*	Forest, shrubland, plantations, gardens, degraded forest
Philautus sp.		*x*									*170*	
Polypedates maculatus	*LC/S*								*x*		*156*	Forest, shrubland, lentic, disturbance tolerant
Psudophilautus sp.		*x*									*170*	Forest, degraded forest.
Raorchestes cf. *ghatei*	*NA*								*x*		*1131-*	
Sphaerotheca dobsonii	*LC/D*					*x*					*85-974*	Lowland forest, shrubland, seasonal lentic
Uperodon globulosus	*LC/S*	*0.07*									*67*	Generalist, anthropogenic environments, disturbance

4.3.1 Caecilian microhabitats on lateritic plateaus

Soil is important for many amphibians providing sites to aestivate but is critical the semi-fossorial caecilians (Kupfer & Himstedt, 2005; Naniwadekar & Vasudevan, 2007; Cortés-Gómez, & Urbina-Cardona, 2013). Three of the 4 caecilian taxa were associated with rocks in addition to areas of soil or stream presence (Tables 4.0-2 & 3). The exception was *Gegeneophis* cf. *ramaswamii*, considered a generalist fossorial taxon, a view this study supports from results associating it with soil-filled depressions (Table 4.0-2 [IUCN, 2016-2]). We observed that *Indotyphlidae* sp, were detected diurnally under lateritic rocks that were positioned on soil depressions indicating the importance of co-occurrence of some microhabitats. These soil depressions were often no deeper than 10 cm. *Gegeneophis* cf. *ramaswamii*, *G. seshachari*, *Indotyphlus* cf. *battersbyi* and *I. maharashtraensis* were all located between the rock and the soil substrate although not significantly for *G.* cf. *ramaswamii*. One single *I. maharashtraensis* at Jagmin was found emerging from a soil depression next to rain fed flowing run-off stream after nearby terrain was disturbed by searching activity. The rocks caecilians were detected under were all within a short distance (no more than 20 m) from surface run-off, stream, or wet seep areas supporting the view soil moisture is likely to be highly important to the group (Lekhak & Yadav, 2012). The *Gegenophis* sp are oviparous and use rocks to shelter their young, for example, *Gegeneophis seshachari* at Kudopi comprised a mixture of adult and juveniles all found under rocks within a single 50m stretch of wet run-off (Giri, Wilkinson & Gower, 2003).

4.4 Discussion

Much literature only describes the broad habitat and not the microhabitats required by the individual taxa for example forest or savannah (IUCN, 2016-2). The distribution of microhabitats on the plateaus in the NWG was non-random irrespective of the scale of observation as their pattern reflects the edaphic processes, macroclimate and disturbance factors at play in the Region (Fig 4.0-2, 3 & 4). The presence and abundance of some of those microhabitats were changed by human activity. All taxa in

the study had identifiable habitat associations, with the majority being significant (Tables 4.0-2 & 3). The study found that each lateritic plateau, whilst having core microhabitat similarities, had a unique habitat and thus identity. Therefore, a macroscale distribution amphibian pattern derived from macroclimate and surrounding countryside alone was imperfect and patch quality in terms of microhabitat availability and thus regulating patch habitat must be included as explanatory factor. We find patch quality, within a climatic zone, was best defined by its microhabitat mix. Some microhabitat availability was directly related to anthropogenic activity. The rarest taxa in the study were the most sensitive to anthropogenic habitat alteration.

The plateaus have localised microclimates and offer habitats, comprised of mosaics of microhabitats, and are at high ecological contrast to the surrounding landscape (Watve, 2013). There is evidence to suggest that has resulted in genetic isolation between plateaus in other taxa (Hanski, 1998; Robin & Nandini, 2012). The resulting amphibian distribution reflects both the isolation and divergent pressure within the WG through the exceptional levels of endemism on the plateaus of the NWG; 61% of the sample were endemic to Asia, 52% to India and 38% to the WG with *Raorchestes ghatei* and *Xanthophryne tigerina* only known from lateritic plateaus (Tables 2 & 3). More common taxa, which we characterise as generalists, are able to move through the countryside between plateaus and can persist on plateaus through metapopulation dynamics (Ficetola & Bernadi, 2004; Schut, et al. 2014; Thorpe & Watve, 2016). Both the common taxa and the rare ones that cannot cross the space between plateaus are reliant upon suitable habitat availability within each plateau (Mortelliti, & Boitani, 2010; Watve, 2013; Thorpe & Watve, 2016). Therefore, habitat quality was highly important in determining the presence and persistence of many taxa but most importantly the rare ones. That quality depends on both landscape level variables including climate, seasonality and topography and within-plateau elements (Deans & Chalcraft, 2016).

Many amphibians use water as their primary habitat to avoid desiccation or predation and as a breeding resource and that was reflected with the majority (67%) of the sample being associated with

water bodies, a figure very close to that published for other areas in the WG (62%), (Tables 4.0-2 & 3 [Aravind & Gururaja, 2011; da Silva, et al. 2012; Cortés-Gómez, & Urbina-Cardona, 2013]). However, non-aquatic microhabitat associations were also found for 78% of the sample taxa (Tables 4.0-2 & 3). Those microhabitats, climatic and habitat combinations fulfil a variety of ecological purposes beyond their basic physiological requirements; refugia from climatic extremes (Smith et al. 1999), and predators (Hartel et al. 2007), mate advertisement perches (Gaitonde, Giri & Kunte, 2016), sites for egg deposition (Chan, 2003; Gaitonde & Giri, 2014), breeding resources (Rittenhouse & Semltisch, 2007; Wells & Schwartz, 2007; da Silva et al. 2012); reproductive behaviour is selected for by suitable rainfall and relative humidity conditions (Hanski, 1998; Gaitonde, Giri & Kunte, 2016; Rittenhouse & Semltisch, 2007).

4.4.1 Seasonal changes in microhabitat use

Many of the plateau taxa breed close to the start of the monsoon and they may have been detected in association with their breeding microhabitats (Daniels, 1992; Gaitonde, Giri & Kunte, 2016). The plateaus are all highly seasonal only receiving rainfall for around four months a year resulting in the need for seasonal movement to avoid desiccation and to access breeding sites (Hanski, 1998; Wells & Schwatz, 2007; Gaitonde, Giri & Kunte, 2016). Rainfall, hydroperiod and the associated relative humidity are important factors for taxa with terrestrial or semi-terrestrial larvae for example *Xanthophryne tigerina* which was found only in the very wet southern high sites (Wells & Schwatz, 2007; Biju, et al. 2009a; Gaitonde, Giri & Kunte, 2016).

4.4.2 Generalist taxa microhabitat associations

Generalist taxa in this study were associated with more than twice as many types of microhabitat than the mean for other taxa (Table 4.0-2). However, the IUCN definition may be spatially too coarse to adequately describe patch quality as it makes little reference to microhabitat associations. There were two non-generalist taxa, *Gegeneophis seshachari* and *Microhyla ornata*, with very similar number of associated microhabitats (4) to the generalist total (3.7) suggesting that they too were generalists.

However, such a result can be explained by co-occurrence microhabitats necessary for some taxa. For example, the microhabitats for *Gegeneophis seshachari* encompass a range predictable for a caecilian; rock, soil and water (Table 4.0-2). Another, *Gegeneophis* cf. *ramaswamii,* was perhaps wrongly identified as a generalist as it appears to require specific combinations of microhabitats to persist but can also be found among a range of landscapes. Similarly, *Microhyla ornata* should be reclassified as a habitat generalist in the context of lateritic plateaus. The generalist taxa, *Duttaphrynus melanostictus* and *Hoplobatrachus tigerinus* each have associations with all three aquatic microhabitats. This was an unsurprising result as both are pond breeding taxa that are also associated with abundant woody plant cover (Table 4.0-2 [Raj, Deepak & Vasudevan, 2011]).

4.4.3 Impact of elevation on microhabitat associations

Tropical site habitats are known to change with elevation a view supported by this study (Fig 4.0-2 & 3 [Fauth, & Slowinski, 1989; Lynch & Duellman, 1980; Gower & Wilkinson, 2005]). The drivers of elevational differences in the amphibian assemblages on the plateaus of the NWG were microhabitats dependent upon rainfall increasing which increased in frequency and volume with increasing elevation and hydroperiod which decreases with latitude. Although not directly related to elevation the ease of access onto low elevation sites, and their agricultural land use, has increased man-made pool frequency and reduced the abundance of large rocks (Fig 4.0-2, 3 & 4). The combination of long periods of rainfall, the related high relative humidity and abundance of loose rocks on Amboli High and to a lesser extent Amboli Low creates a special habitat the critically endangered and declining Amboli Toad, *Xanthophryne tigerina*. The large rocks provide three major resources, refugia, breeding sites and mate advertisement sites (Gaitonde, Giri & Kunte, 2016). All of these are highly important resources for not only *X. tigerina, but* as breeding sites for Caecilians (Gower & Wilkinson, 2005). Woody plant abundance was one of the main microhabitats to define the regional difference between the high and low-level sites (Fig. 4.0-3 & 4). Together with its associated soil filled depressions woody plants were highly important in amphibian distribution on the NWG plateaus across all elevations but impacting different taxa (Tables 4.0-2 & 3).

4.4.4 The effect of anthropogenic disturbance on amphibian microhabitats

Microhabitat availability was changed by three forms of anthropogenic disturbance on the plateaus; removal e.g. loose rocks, damage e.g. trampling or cutting down of plants and alteration by addition of foreign material e.g. soil at Panchami. Anthropogenic disturbance was also evidenced by construction and pollution. We did not examine the impact of addition by construction, pollution or trampling and therefore cannot comment specifically on these, although the sites with wind turbines had some construction on them. All rural communities close to the plateaus carried out the common practice of harvesting loose rock and utilising it for construction of dwellings, walls and memorials (Watve, 2013). Therefore, sites at which there were quantities of rocks >50 mm^3 were often farther from human residences. Given that many of the amphibian taxa in this study were associated with, detected under, or proximate to cover provided by rocks >50 mm^3 we suggest that the natural occurrence of rocks >50 mm^3 on plateau sites is an essential microhabitat resource for all amphibians, and one that is a rapidly emerging conservation concern for all plateaus.

Disturbance by the addition of soil, together with tourist related activity; on the high-level site Panchgani has shifted the taxa assemblage towards one dominated by generalist or widely distributed taxa (Tables 4.0-2 & 3). The addition of soil has closed almost all the fissure refugia and all large loose rocks and most small ones have been removed, limiting the available types of refugia, breeding and mate advertisement sites. This site is popular with equine tourism and this local industry has resulted in infrastructure development (cafes, stables and roads), soil compaction and increasing levels of domestic refuse. The pools also have a high silt load from the imported soil and grazing. A total of 24 individual amphibians were recorded from this plateau. Although amphibian counts were relatively high in comparison to lower disturbance sites, several of the taxa recorded (*D. melanostictus, E. cyanophlyctis* and *H. tigerinus*) are considered widespread or generalist taxa, listed as "least concern" in the IUCN status reports (Tables 4.0-2 & 3). *D. melanostictus*, *E. cyanophlyctis* and *H. tigerinus* were anticipated as taxa known to associate with anthropocentrically disturbed or

modified habitats (Daniel, 2002). However, the presence of *Raorchestes* cf. *ghatei* and *Fejevarya* cf. *brevipalmata* may be surprising as they had limited distribution and are data deficient taxa in need of more robust ecological and population studies (Tables 4.0-2 & 3). Panchgani has a number of large pools constructed for watering livestock and anthropogenic uses. The largest is likely to hold some water throughout an average year possibly shaping the community by offering aquatic refugia in the dry season not seen on many sites. That may be a significant factor structuring the assemblage as it would favour pond specialist taxa (Scheffer et al. 2006).

Surface topography on the low-level plateaus creates some pools but many additional ones have been created by farmers in association with their agricultural land use. At a landscape level pool frequency is important in maintaining population connectivity and persistence (Oertli et al. 2002, Scheffer et al. 2006, Jocqué et al. 2007).

4.4.5 Climate change and the amphibians of the northern Western Ghats

Two changes in climate are predicted to impact the amphibian microhabitat requirements in the NWG: increasing temperature and fragmentation of the monsoon rains (IPCC, 2014). Both will require microhabitat resources to mitigate their effects; as refugia from increased temperatures and desiccation (Scheffers et al. 2014; Schut et al. 2014). The woody plants and rocks in this study provide thermal refugia allowing behavioural temperature regulation and are therefore key microhabitats worthy of preservation (Scheffers et al. 2014). Breaks in rainfall that occur when larvae are in pools or in hygropetric habitats are likely to cause significant losses. To offset these, maximum availabilities of both populations and microhabitats should be preserved.

4.5 Conclusion

We conclude that microhabitat availability is a good way of defining patch quality for amphibians within a climatic zone and preserving patch quality is important for conserving amphibians. The study, as the first statistically supported in the NWG, has added substantially to known amphibian

microhabitat associations. Spatial variation in microhabitat distribution in part explains amphibian diversity on the threatened lateritic plateaus in the NWG. The preservation of a wide a range of microhabitats is clearly important for amphibian conservation. It is clear that the NWG lateritic plateaus, with their unique microhabitat assemblages, are highly important habitats for a significant number of threatened amphibians and conservation policy should aim to preserve representative plateaus from each Eco-zone. Preservation of microhabitats that provide thermal and desiccation refugia will become increasingly important for the persistence of plateau amphibians in the face of increasing temperatures and a more fragmented monsoon; these include pools, large rocks and woody plants (Frishkoff, Hadly & Daily, 2015).

Chapter 5. Climate structuring of *Batrachochytrium dendrobatidis* infection in the threatened amphibians of the northern Western Ghats, India.

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Author contributions: CJT Designed and implemented the study and authored the paper: TRL assisted with the study design, data collection, taxonomy and editing; MCF and CJW helped with molecular analysis; DTB assisted with study design; SK assisted with logistics; DP and LD assisted with data collection; DTB assisted with study design, taxonomy and editing; AW assisted with permits and fieldwork; MEK assisted with study design and editing.

Abstract

Batrachochytrium dendrobatidis *(*Bd*) is a pathogen killing amphibians worldwide. Its impact across much of Asia is poorly characterised. This study systematically surveyed amphibians for Bd across rocky plateaus in the northern section of the Western Ghats Biodiversity Hotspot, India, including for the first surveys of the plateaus in the coastal region. These ecosystems offer an epidemiological model system since they are characterised by differing levels of connectivity, edaphic and climatic conditions, and anthropogenic stressors. One hundred and eighteen individuals of 21 species of Anura and Apoda on 13 plateaus ranging from 67-1179m above sea level and 15.89 to 17.92° North Latitude were sampled. Using qPCR protocols 79% of species and 27% of individuals tested were positive for* Bd. *This is the first record of* Bd *in caecilians in India, the Critically Endangered* Xanthophryne tigenrinus *and Endangered* Fejervarya cf. sahyadris. *Mean site prevalence was*

28.15%. Prevalence below the escarpment was 31.2% and 25.4% above. The intensity of infection (GE) showed the reverse pattern. Infection may be related to elevational temperature changes, thermal exclusion, inter-site connectivity and anthropogenic disturbance. Coastal plateaus may be thermal refuges from Bd*. Infected amphibians represented a wide range of ecological traits posing interesting questions about transmission routes.*

5.1 Introduction

Batrachochytrium dendrobatidis (Bd) (Longcore, Pressier & Nichols, 1999) is an aggressive species of chytrid fungus that can cause the lethal amphibian infection chytridiomycosis (Olson et al. 2013). Following the emergence of a hyper virulent lineage of *Bd,* the Global Panzootic Lineage *Bd*GPL (Farrer et al. 2011), in the early 20th Century, the pathogen has been responsible for the loss of entire species (Fisher et al. 2011) and is considered a significant threat wherever it is found (Rödder, et al. 2009). The presence of *Bd* in the Western Ghats Biodiversity Hotspot (WG) (Myers et al 2000) has been known since 2011 (Nair et al 2011) with its known range in the WG extended in 2015 (Molur et al. 2015) and chytridiomycosis was reported from the northern WG in 2013 (Dahanukar et al. 2013). It was identified as an endemic Asian strain in 2013 (Dahanukar, et al. 2013). It remains unclear what factors regulate the distribution of *Bd* in the WG, its transmission, or the reasons for its current generally sub-lethal state in the region. In a peculiar twist of fate areas that are home to the world's greatest amphibian diversity are also most susceptible for *Bd* (Ron, 2005). In a global model Olson et al. (2013) found the entire WG suitable habitat for the pathogen (Olson et al. 2013).

The Western Ghats (WG) in southwest India occupy just 5% of the country's land mass and yet are home to some 42% of its amphibian species (~161 species [Aravind & Gururaja, 2011; Giri, 2016]). Not only are the WG highly specious but many of its amphibian species are rare, with 87% being WG

endemics (Giri, 2016). The amphibians that are endemic to the rocky plateaus (plateaus) face both proximate and ultimate threats including; climate change (IPCC, 2014), and regional stressors population growth (Cincotta, Wisnewski & Engelman, 2000), along with rapid habitat loss through mining, tourism, and wind turbine installations (Bharucha, 2010; Kasturirangan, et al. 2013; Watve, 2013; Thorpe & Watve, 2016). They also face challenges from pathogens such as the fungus *Batrachochytrium dendrobatidis (Bd)* (Nair et al. 2011; Dahanukar et al. 2013; Molur et al. 2015). Systematic studies on *Bd* in Asia are under-represented in the literature (Whittaker & Vredenburg, 2011) and this study aims to help to address that shortfall.

The three studies that have been published so far examining *Bd* infection in the Western Ghats Biodiversity Hotspot (WG), cover almost the entire length of the WG and report widely differing levels of infection ranging from 0.6% (Nair et al. 2011) to 25% (Dahanukar et al 2013). The most geographically extensive study, covering the northern, central and southern WG, reported an infection rate of 1.6% (Molur, et al. 2015). All three studies excluded the low-lying sites between the coast and the hills. Molur et al. (2015) published a predictive model showing higher risk of infection south of ~14.5°N in the central section of the WG.

This present study adds considerably to the previous WG publications by surveying low elevation sites for the first time. In addition, this is the first study in the WG to offer data on habitat specific infection rates, and infection patterns across a wide range of elevations. Such data are highly important as the high-level plateaus are becoming recognised as centres of endemism for a number of taxonomic groups and data on all threats are urgently needed for their effective management (Bharucha, 2010; Whittaker & Vredenburg, 2011; Kasturirangan et al. 2013; Poermbski et al. 2016).

5.2 Methods

5.2.1 Study Area

The WG are a chain of hills some 1500km in length running parallel and slightly inland from the south west coast of India from the Maharashtra/Gujarat state border to the country's southern tip (Fig 1.0-1 & 4). They are part of the Western Ghats-Sri Lanka Biodiversity hotspot (Myers et al. 2000) and the 8th 'hottest' hotspot on the planet (Sloan et al. 2014). Unlike the granitic central and southern sections, the northern section in western Maharashtra, known as the Deccan Traps (DT), is formed from basalt. The plateaus are ferricretes of laterite forming hilltop carapaces above the escarpment on the western edge of the WG rising to 1200m above sea level (m), with extensive low-lying plateaus below it in an area known as the Konkan (Widdowson & Cox, 1996). These range from 15°-40°C in the Konkan and 4°-42° above the escarpment (Watve, 2010). The higher elevation amphibian populations are exposed to lower temperatures that may be more conducive to *Bd* infection (Laurance, McDonald & Speare, 1996).

5.2.2 Amphibian sampling

Amphibians were sampled from 13 representative plateaus situated in the northern WG both above and below the North-South escarpment in western Maharashtra during the early monsoon in 2013 and 2014; late July-early August (Fig. 1.0-4; Table 1.0-3). Plateaus were selected to represent the latitudinal and elevation extent of laterite in western Maharashtra together with the range of land uses in each Region (Fig 1.0-2; Table 1.0-3). Visual encounter surveys with supplementary refugia searching were performed along four 6m by 100m transects on each plateau in each year (Crump & Scott, 1994; Vonesh, et al. 2010). Anthropogenic disturbance factors assessed at each site were; removal of loose rocks, surfaced road, unsurfaced road, built structures on the plateau, domesticated animal grazing, surfaced road within 200m of plateau, tourism, part conversion to plantation, adjacent built structures, importation of topsoil. Sites with 0-3 factors were considered to have low levels of disturbance, those with 4-7 Medium Disturbance and with 8+ High Disturbance (Table A.3.3).

Sampled amphibians were identified by morphological comparison with the best literature available, including (Bhatta, 1998; Dubois, Ohler & Biju, 2001; Bossuyt, 2002; Giri, Wilkinson & Gower, 2003; Biju & Bossuyt, 2009; Biju & Bossuyt, 2009a; Biju et al. 2009; Daniel 2002; Giri, Gower & Wilkinson, 2004; Kuromoto & Joshy, 2003; Kuromoto et al. 2007; Dinesh et al. 2009; Dinesh et al. 2015; Dahanukar et al. 2016; Garg & Biju, 2016; Dinesh et al. 2017; Frost, 2017; Garg & Biju, 2017). Many WG amphibians are taxonomically cryptic or unstable (Dahanukar et al. 2016; Garg & Biju 2016; Garg & Biju 2017); in cases where species-level identification may be in doubt we use 'cf.'.

5.2.3 Field sampling and laboratory techniques

Amphibians were all hand-captured, individually bagged and transported to shelter where skin swabs were taken from ventral surfaces. Swabbing was performed by a pair of surveyors using sterile cotton tip swabs (T/S16-B; Technical Service Consultants Ltd [Brem, Mendelson & Lips 2007; Hyatt et al. 2007]). The ventrum, drink patch, thighs and toe-webbing of each adult anuran and metamorph was swabbed multiple times following published standardised protocols (Vredenburg, 2009). For caecilians a simpler approach of multiple swab strokes along the whole of the body was used. Swabs were broken off into sterile vials of 99% ethanol. Disposable equipment (latex gloves and polythene bags) were replenished between specimens and sites. Other equipment was sterilised using VirkonS™ solution or dried to minimise cross-contamination.

DNA extraction from the swabs followed the protocol described in Boyle et al. (2004) (Boyle, et al. 2004; Boyle, et al. 2007). A quantitative real-time polymerase chain reaction (qPCR) diagnostic assay was used with *Bd* specific probes for the ribosomal gene region ITS-1/5.8S (Boyle, et al. 2004). The qPCR was run on Applied Biosystems QuantStudio 7 Flex Real-Time PCR System with an additional 10 cycles being added to the Boyle protocol (60 cycles total). Standards of known concentration *Bd* DNA (100, 10, 1, 0.1 *Bd* GE [zoospore Genomic Equivalents' (GE)]) were used as positive controls and standards together with no template control (NTC) of molecular grade water as a negative control.

The samples were run in duplicate with single positives repeated. A positive result was a sample with a GE greater than 0.1 in both samples in a qPCR pair, a single was a sample with only one of each qPCR pair had a GE >0.1 and a weak signal was where only 1 out of 4 qPCR scores was >0.1.

5.2.4 Environmental correlates

Bd is sensitive to a range of changes in the abiotic environment. Plateau soils are acidic ranging from below pH 4.9 which is lower than the *Bd* optimum of pH 6-8 (Watve, 2010; Watve, 2013; Piotrowski, Annis & Longcore,, 2004). In addition, *Bd* is temperature-sensitive growing best between 17 and 25°C, with an optimum of 23°C (Piotrowski, Annis & Longcore 2004; Pounds et al. 2006). Temperature may also regulate the pathogenicity of *Bd* with frogs exposed between 17 and 23°C more likely to die than those exposed at 27°C (Berger et al. 2004). The fungus is reported to die when the temperature exceeds 30°C, a level exceeded at times on all plateaus (Ron, 2005; Watve, 2013). Lower seasonal temperatures, such as those during the monsoon at higher elevations in the WG, are known to favour the pathogen (Piotrowski, Annis & Longcore 2004). The plateaus are mosaics of microhabitats set in a heterogeneous landscape with unknown degrees of connectivity for *Bd* (Ghalambour et al. 2006; Watve, 2010; Watve, 2013; Thorpe & Watve, 2016). Microhabitats include expanses of exposed rock often with associated loose rocks. Exposed rock absorbs solar radiation giving it a surface temperature higher than the air, perhaps creating microclimates that may reduce the intensity and presence of the pathogen (Puschendorf et al. 2011). Other microhabitats include loose rocks and fissures offering refugia from dry areas and excessive temperatures (Puschendorf et al. 2009; Voyles et al. 2012; Thorpe et al. 2018). Optimum rainfall for *Bd* is reported to be between 1500 and 2500mm a year. Only the low-lying plateaus fall within this range, the plateaus along the top of the escarpment receiving between 4000 and 9000mm, with the exception of Masai which is east of the ridge and may be drier (Ron, 2005; Thorpe et al. 2018).

Macro-environment and physiochemical data were recorded for each site: air, soil and water temperature (°C) and pool pH using a calibrated electrical probe (Hanna Instruments™ HI 9064);

elevation (m) latitude and longitude for the start and end of each transect using a hand-held GPS (Garmin™ 60csx GPS).

5.2.5 Permission for fieldwork

Permission for accessing biodiversity in India including the fieldwork was granted by the National Biodiversity Authority, India, to C. J. Thorpe permit number MC200621. The permit authorises some other authors to assist with sampling.

5.2.6 Data analysis

For analytical comparison the northern WG study area which is divided into High (>650m above sea level (m) and Low Regions (<700 m) separated by the Western Ghats escarpment and into 3 arbitrary latitudinal groups North, Central and South (Table A.3.3). Correlations between site elevation, temperature and pH were explored through Pearson Product Moment Correlation for parametric data and Spearman Rank Correlation for non-parametric data. To assess the impact of the spatial arrangement and disturbance on *Bd* GE values, General Linear Model and one-way ANOVA analyses were performed to investigate elevation, latitude, Region, disturbance type and disturbance intensity. Results are reported with a Confidence Level of 95% (CL) together with upper and lower bi-nomial Confidence Bounds (CB) which are the outer values of the confidence interval and are expressed as percentages (Vogt & Johnson, 2011; Maestri et al. 2018).

5.3 Results

5.3.1 Overview of *Bd* infection in the study area

A total of 118 sample swabs were taken from individuals belonging to 2 orders, 6 families, 14 genera and 19 taxa (Table 5.0-1). Seventy nine percent of the taxa tested had positive individuals for *Bd*

(Table A2.3). The study does not provide an inventory of infection for the area as it only covered one ecosystem and complete detection of both species and infection is problematic (Guimarães, & Munguía-Steyer, 2014). Total prevalence in the sample was 11% (95% CL; CB 7-19) if single positives were included 22% (95% CL; CB 15-31) and 27% (95% CL; CB 19-36) including weak positives. As in other WG studies, all GE values recovered were low and all those with a single GE value >0.1 were included in the analysis (Table 5.0-1 [Nair et al. 2011; Dahanukar et al. 2013; Molur et al. 2015; Clare et al. 2016]).

All four species of caecilian found in the study were infected (Table 5.0-1). The critically endangered Amboli Toad, *Xanthophryne tigerina*, was infected with low prevalence (6.7%; 95% CL; CB 1-32) as were 33% of the endangered frog *Fejervarya* cf. *sahyadris* in the sample (95% CL; CB 13-65) (52). One site, Amboli High, returned no positives out of 6 *Xanthophryne tigerina* samples. Amboli High was the only site without any positive results. No amphibians were detected with external signs of chytridiomycosis.

5.3.2 Spatial distribution of *Bd* infection

Site prevalence varied between 0 and 50% and species infection rate 0-60% (Table 1; S1 Table 4). Macroscale variations in GE values were found with the Regions exhibiting a significant tenfold difference in mean GE (ANOVA, $F_{1,2}$=3.99, p=0.06 [Fig. 2a & b]). The Low Region had more infected individuals (56%; 95% CL; CB 26-62) than the High Region (44%; 95% CL; CB 37-56). Individual GE value increased with elevation (ANOVA, $F_{11,20}$=4.85, p<0.01).

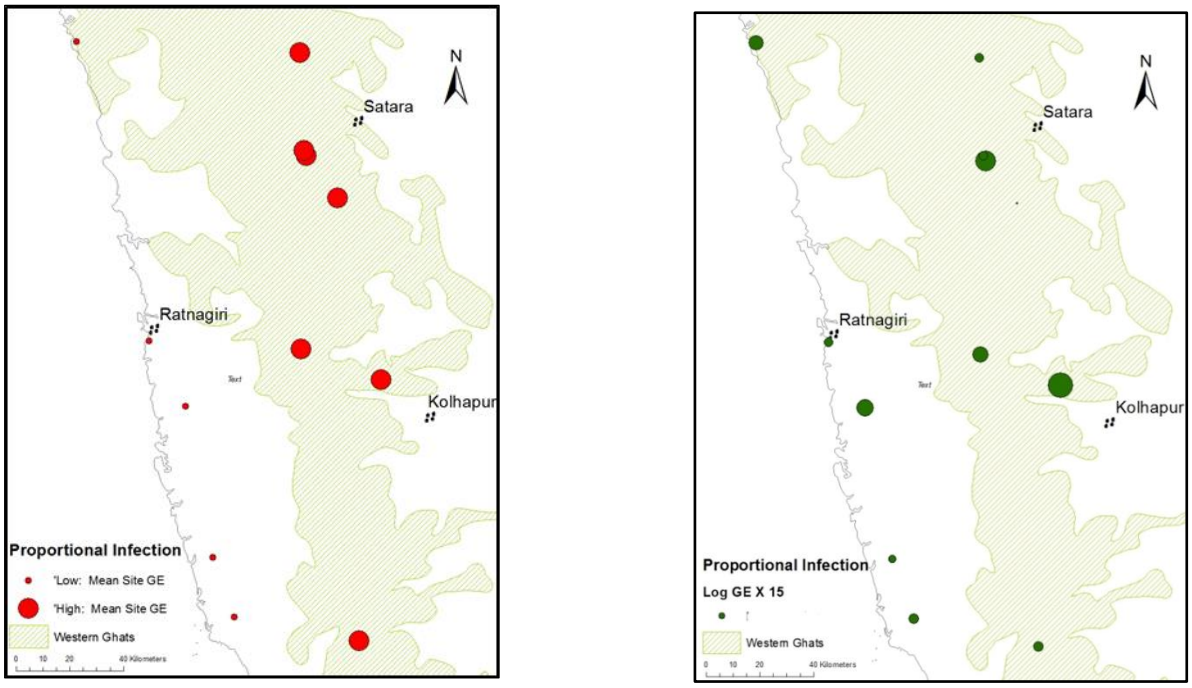


Figure 5.0-1a & b. The left hand figure illustrates the proportional difference in Regional values of mean site GE values. The right hand illustrates the individual site mean GE.

Table 5.0-1. Taxonomy, risk and infection as prevalence. Where nomenclature is uncertain the rules of the International Code of Zoological Nomenclature (ICZN) have been followed. Where identification is hampered by cryptic species a most likely identity is shown with the prefix 'cf'. IUCN threat status and known habitat associations accessed 10/02/2017 (IUCN 2016-2). NA- Not Assessed; DD-Data Deficient; LC-Least Concern; EN-Endangered; CR-Critically Endangered. n is the number of individuals in the sample. Prevalence is the percentage of the sample tested positive for Bd.

Order	Family	Genera and Species	IUCN	n	Prevalence	95% CL
Anura	Bufonidae	*Duttaphrynus melanostrictus*	LC	7	43	0.09-0.82
Anura	Dicroglossidae	*Euphlyctis* cf. *cyanophlyctis*	LC	2	0	0-0.84
Anura	Dicroglossidae	*Fejervarya* cf. *brevipalmata*	DD	9	11	0.01-0.48
Anura	Dicroglossidae	*Fejervarya* cf. *caperata*	DD	4	75	0.19-0.99
Anura	Dicroglossidae	*Fejervarya* cf. *cepfi*	NA	7	14	0.01-0.58
Anura	Dicroglossidae	*Fejervarya* sp.		10	33	0.07-0.65
Gymnophiona	Indotyphlidae	*Gegeneophis* cf. *ramaswamii*	LC	5	20	0.01-0.72
Gymnophiona	Indotyphlidae	*Gegeneophis seshachari*	DD	9	44	0.14-0.79
Anura	Dicroglossidae	*Hoplobatrachus tigerinus*	LC	9	56	0.21-0.86
Anura	Ranixalidae	*Indirana* cf. *chiravesi*	LC	3	33	0.01-0.91
Gymnophiona	Indotyphlidae	*Indotyphlus* cf. *battersbyi*	DD	2	50	0.01-0.99
Gymnophiona	Indotyphlidae	*Indotyphlus maharashtraensis*	DD	3	33	0.01-0.91
Anura	Microhylidae	*Microhyla ornata*	LC	1	0	0-0.98
Anura	Dicroglossidae	*Fejervarya* cf. *sahyadris*	EN	14	36	0.13-0.65
Anura	Rhacophoridae	*Phseudophilautus* sp.		1	0	0-0.98
Anura	Rhacophoridae	*Raorchestes* cf. g*hatei*	NA	5	60	0.15-0.95
Anura	Dicroglossidae	*Sphaerotheca dobsonii*	LC	5	20	0.01-0.72
Anura	Microhylidae	*Uperodon globulosus*	LC	1	0	0-0.98
Anura	Bufonidae	*Xanthophryne tigerina*	CR	15	6.7	0.01-0.32

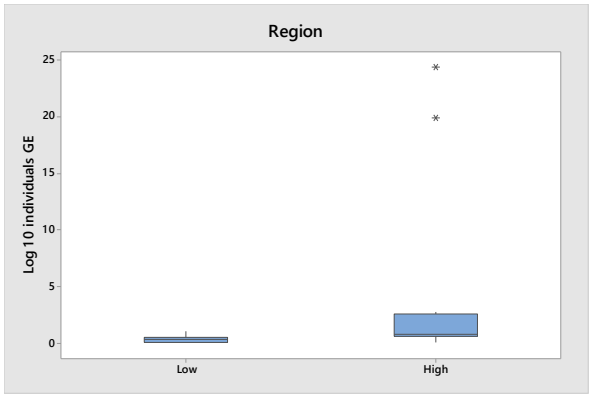
5.3.3 Environmental relationships with *Bd* infection

As both water temperature and pH co-varied with elevation, and pH with water temperature, elevation alone was used to explore spatial relationships (Table A.3.1). Temperature in the Low Region had a notable maximum of 36.4°C (mean 30.9°C) much higher than above the escarpment 28.3°C (mean 22.5°C; minimum 19.3°C [Table A.3.2]). Both Regions had minimum pH values below the *Bd* optimum although mean values were within the pathogens tolerance range (Tables 5.0-2 & A.3.2).

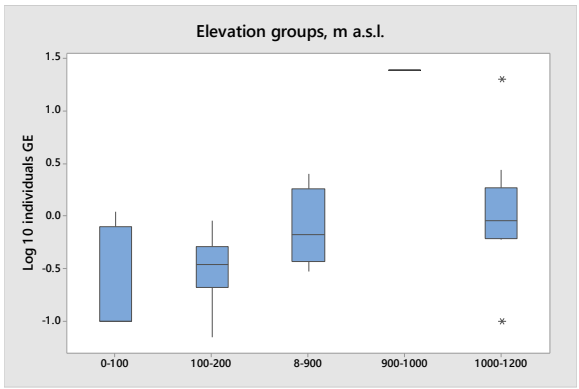
GLM ANOVA analysis was used to assess the factors regulating the distribution of infection intensity (Fig 5.0-2 a-e). Plateau elevation had the greatest impact showing an upward trend with elevation (Fig 5.0-2b). Land-use was the second most crucial factor, agriculture had a negative impact on sites below the escarpment, and above the escarpment the type of land-use did not have a clear impact (Fig 5.0-2c). The intensity of disturbance was related to an increasing trend in infection intensity (Fig 5.0-2d). Latitude, which includes Low and High Region sites in each class, suggests a limited decreasing trend with increasing latitude (Fig 5.0-2e).

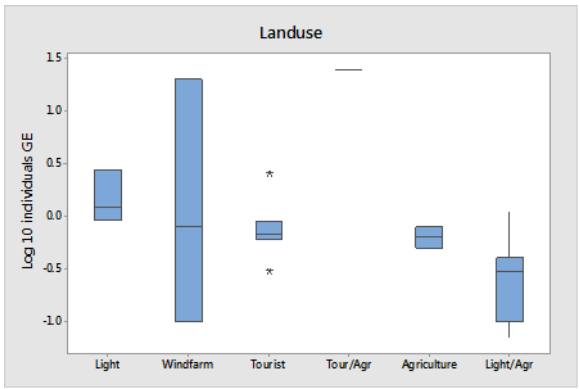
Table 5.0-2. Physio-chemical parameters described for the survey area and the two Regions. Temperature = Water Temperature in °C.

Variable	Region	Mean	Minimum	Maximum
Temperature	Low	30.9	26.2	36.4
Temperature	High	22.5	19.3	28.3
Temperature	All	24.8	19.3	36.4
pH	Low	6.7	5.0	9.6
pH	High	7.6	5.3	12.2
pH	All	7.3	5.0	12.2

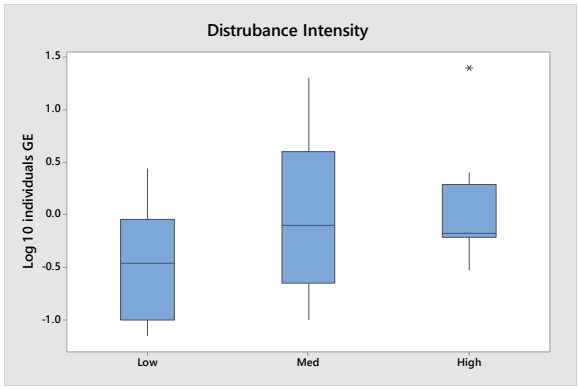


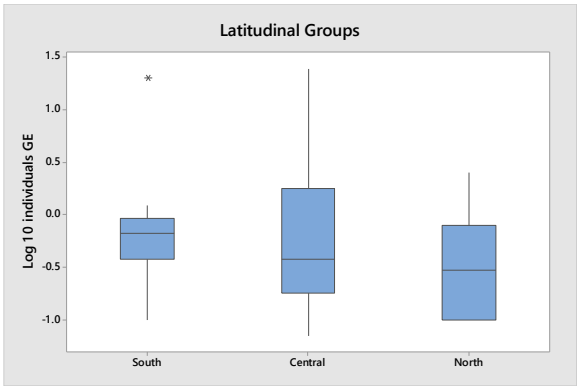
a)





b) c)





d) e)

Figure 5.0-2 a-e. Box and whisker plots for Log_{10} Transformed GE data for individuals. Quartile 2 and 3 shaded with the dividing line as the median. The whiskers are Quartile 1 and 4. Outliers are indicated by asterisks. GLM ANOVA; a) Inter-Region b) Elevation Groups, $F=12.77$, $df_{factor}=1$, $df_{error}=24$, $p<0.01$; c) Land-use, $F=10.88$, $df_{factor}=1$, $df_{error}=24$, $p<0.01$; d) Disturbance Intensity, $F=2.99$, $df_{factor}=4$, $df_{error}=24$, $p<0.05$; e) Latitudinal Groups, $F=3.33$, $df_{factor}=1$, $df_{error}=24$, $p=0.08$.

5.4 Discussion

There was widespread but low intensity infection of *Bd* in almost all the plateaus sampled except for one, (Amboli High), and in 79% of the amphibian species examined on the rocky plateaus in the northern WG (Table 5.0-1). These are the first records of infection in the critically endangered Amboli Toad, *Xanthophryne tigerina;* the endangered frog *Fejervarya* cf. *sahyadris;* and four species of Caecilian *Gegeneophis* cf. *ramaswamii; Gegeneophis seshachari; Indotyphlus* cf. *battersbyi* and *Indotyphlus maharashtraensis* (IUCN, 2016-2). Three of the caecilian species are described by the IUCN as data deficient (Table 5.0-1). Infection was detected in two species yet to be assessed by the IUCN; *Fejervarya* cf. *cepfi; Raorchestes* cf. *ghatei* and two other data deficient species *Fejervarya* cf. *brevipalmata* and *Fejervarya* cf. *caperata* (Table 5.0-1). This is the first study to investigate *Bd* infection in low lying coastal sites, where there was higher prevalence but lower intensity infection than on sites above the WG escarpment (Fig 5.0-1a & b; Fig 5.02a). Site elevation, with its covariables, and disturbance intensity, were the most significant explanatory factors in the pattern in *Bd* distribution (Fig 5.0-2b & c). Although another explanation, not explored here, for the observed pattern in *Bd* distribution is that the amphibian populations are relics of ancient dispersals isolated from the pathogens transmission vectors (Weinstein, 2009).

5.4.1 Low elevation plateaus are less conducive to Bd but with greater connectivity

Puschendorf et al. (2011) suggest that disease-free amphibian refuges are created in drier areas with temperatures above those tolerated by *Bd* (Puschendorf et al. 2011). We suggest our findings, with lower infection intensities on the Konkan plateaus, support them as a possible refugia for some amphibian species from *Bd*. However, the higher prevalence on plateaus below the escarpment are more difficult to explain. The plateau specific environment derived from their open habitat may have created thermal refugia from *Bd* in rock pools and surrounding habitats where temperatures exceed the pathogens upper thermal tolerance, but it should also restrict transmission. The pools are scattered

across plateaus with surface temperatures, especially on the exposed rock, greatly more than the pathogens thermal maximum, which should restrict the pathogens persistence and transmission (Watve, 2010; Retallick, McCallum & Speare, 2004).

Low Region water temperatures were higher than those above the escarpment, on average 30.9°C, with a maximum 36.4°C, a figure well above published critical zoospore thermal thresholds of 23-28°C (Table 5.0-2; Fig 5.0-2a; Table A.3.1 & 2 [Piotrowski, Annis & Longcore, 2004; Ron, 2005; Olson et al. 2013; India, 2017]). Even more lethal are the rock surface temperatures which can exceed 50°C (Watve, 2010). The Region is also drier, with less rain and fewer wet days than above the escarpment. The annual rainfall falls within the pathogens preferred rainfall range of 1500-2500 mm but it only rains for five months a year, with the remaining seven months being almost completely dry with very low relative humidity (Ron, 2005; Watve, 2010; IMD, 2016; India, 2017). Infection intensity decreased slightly with increasing latitude possibly reflecting the latitudinal decline in the number of wet days (Fig 5.0-2e [Puschendorf et al. 2009; Voyles et al. 2012; IMD, 2016]).

Regional differences in habitat and micro-habitat availability may also help explain the pattern in *Bd* distribution, through behavioural mitigation where amphibians move to, or persist on, plateaus with micro-habitats that are refugia from *Bd* (Lips et al. 2006; Voyles et al. 2012; Thorpe et al. 2018). Conversely stream micro-habitats offer one possible transmission route in the Low Region, where streams are more frequent (Thorpe et al. 2018). Sub-tropical stream-breeders are more susceptible to *Bd* and may be disease vectors with the pathogen spreading from streams into the terrestrial realm (Lips et al. 2006; Scherer et al. 2009). Increased landscape connectivity in the Low Region, resulting from lower inter-site variation in elevation (Low Region 103m, High Region 370m), may enable greater inter-site transmission through amphibians dispersing between plateaus, explaining the higher prevalence and supporting the findings of Heard et al. (2015), (Table A.3.1 & 2 [Janzen, 1967; Ghalambour et al. 2006]). The picture is complex though as some refugia such as woody plants and

large loose rocks may enable behavioural avoidance of excessive temperatures for both amphibians and *Bd* (Pounds et al. 2006; Scheffers et al. 2014 Heard et al. 2015). An idea possibly supported by the results for the four species of caecilian in the study which have similar prevalence to non-fossorial taxa (Table 5.0-1). They are frequently found under loose rocks where temperatures are tolerable for *Bd* and are close to streams which may be used by stream-breeding Anuran vectors (Lips et al. 2006; Thorpe et al. 2018).

5.4.2 *Bd* in the High Region

Despite the High Region offering a more equitable temperature range for *Bd* mean 22.5°C, within the pathogens *in vitro* optimum of 17-25°C, prevalence was less than below the escarpment where the pathogens upper limit was often exceeded. Suggesting the High Regions greater topographical heterogeneity produces barriers to transmission explaining the lower number of infected individuals (Table 5.0-1 & 2; A.3.2; Fig 5.0-1a & b; Fig 5.0-2a & b [Piotrowski, Annis & Longcore, 2004; Ron, 2005; Pounds, et al. 2006]).

Individual GE loadings were greater above the escarpment reflecting the High Regions optimal temperature (Table 5.0-1 & A.3.2 [Ron, 2005; Pounds, et al. 2006]). Whilst excessive temperatures below the escarpment may regulate the pathogen through mortality the High Regions' lower temperature regime may encourage *Bd*, even when the temperature falls below the organisms' lower optimum value (17°C). A temperature of 4°C was used by Voyles et al. (2012) as their minimum in a study assessing the impact of temperature regimes on *Bd* life history; the same minimum temperature was also recorded by Watve (2010) on High Region plateaus. Their lower temperature regime resulted in extended zoospore longevity meaning zoospore numbers in water bodies could be expected to be greater than in warmer pools. The trait may lead to greater encounter rates and thus infection prevalence contrary to our findings (Voyles et al. 2012). However, they also found their low

temperature regime increased zoospore production which offers a plausible explanation for the elevated site GE values in the High Region.

5.4.3 The impact of anthropogenic disturbance on *Bd* distribution

Elevated prevalence close to human settlement is to be expected but with unknown causes (Bosch et al. 2011). The study found that Low Region plateaus, which are less isolated from human settlement, had higher prevalence than their more isolated High Region counterparts (Bosch et al. 2011).

In addition to proximity of human habitation, changes in land-use influences amphibian distribution, and possibly their susceptibility and exposure to disease (Cortés-Gómez, Castro-Herrera, Urbina-Cardona, 2013; Newbold et al. 2014; Thorpe et al. 2018). Sites near human habitation are likely to have anthropogenic land-uses. We found land-uses were different either side of the escarpment. Land-use had an impact on mean individual infection intensity with Low Region agricultural sites having higher infection intensity than the nearest sites with limited disturbance (Fig 5.02c). Land-use in the High Region had a negligible impact on mean individual infection levels (Fig 5.02c). Sites with little disturbance, on our arbitrary scale, had lower mean individual GE compared to plateaus with higher disturbance (Fig 5.0-2d). The actual mechanisms remain unclear, but we can support anthropogenic disturbance as a negative factor in *Bd* infection. The sites disturbed by tourism had amphibian assemblages dominated by generalist species, but this had no impact on mean individual infection intensity suggesting mobile species may not be pathogen vectors (Thorpe et al. 2018).

The impact of disturbance on *Bd* infection intensity was less than that of elevation (Fig 5.02b, c & d). Site prevalence did not reflect land use (Table 5.0-1; Fig 5.0-2b-e). As all the sites with tourism were above the escarpment and elevation had the greater explanatory power, we believe spatially driven climate has more effect than land-use. There is a clearer indication agriculture negatively impacts infection intensity as seen in our Low Region sites where there is little inter-site variation in elevation but a significant difference in infection intensity (Fig 5.0-2c).

5.5 Conclusion

It is clear the *Bd* pathogen is very widely distributed in this area and anthropogenic land-use increase the infection risk. The infected plateau amphibians include several threatened and poorly understood species whose infection we record for the first time. None of the individuals that tested positive for *Bd* showed any external signs of chytridiomycosis. The disease has been reported in *Nyctibatrachus humayuni* from sites close to the northern edge of this survey (Dahanukar et al. 2013). The infection level reported here is well below the mortality threshold of 1-10,000 zoospores (Vredenburg et al. 2010) and is more indicative of an historical infection, or species that are carriers that do not go on to develop chytridiomycosis (Daszak, Cunningham & Hyatt, 2003; Ouellt, et al. 2005; Padgett-Flohr, Hopkins, 2009). The triggers for this low intensity infection to develop into a lethal outbreak of chytridiomycosis are unknown.

Transmission vectors are poorly understood globally as well as in the WG, but we would support the possible explanation of water birds as vectors with lapwing species (*Vanellus indicus*) being frequently observed on all the plateaus (Garmyn et al. 2012). Proximity to human habitation is a risk factor but the mechanisms of transmission are unknown.

Until there is a better understanding of the mechanisms triggering benign *Bd* infection to become lethal chytridiomycosis, its presence should be considered in all future conservation policy decisions. Preservation of dispersed populations on sites with refugia properties, good connectivity and preservation of refugia on individual plateaus is essential in offering the best prospect of long term species persistence (Heard et al. 2015; Heard et al. 2017). The need for further work on modelling infection on a wider scale, especially in the low lying coastal areas, characterised here for the first time for *Bd*, is a priority. A study into the evolutionary history of *Bd* in the entire WG area would also help with its management. There is an urgency to determine the routes of transmission and triggers for

the pathogen to become lethal. That urgency is illustrated by the 2015 publication of the addition of *Duttaphrynus melanostictus* to *Hoplobatrachus tigerinus* as invasive species in another biodiversity hotspot, Madagascar, (82). Both of these species had high *Bd* prevalence in this study; 43% and 56% respectively. Resolution of these questions may be helped by a better understanding of the historical lineage of the *Bd* strain in the WG.

5.6 Research ethics

Advice was sought from the University of Plymouth Animal Welfare and Ethics Committee representative who advised that no formal consent was required since the swabs were non-invasive, collected from external swabbing only. Further they advised following strict international handling protocols and these are described under Methods. Sampling was undertaken by kind permission of the National Biodiversity Authority, Chennai, India under permit number: Maharashtra 2014 MC200621.

Chapter 6. Sky islands: the role of isolation, elevation and land-use in shaping ant (Formicidae) assemblages across an archipelago of subtropical rocky plateaus, Western Ghats, India.

C. J. Thorpe, D.T. Bilton, S. Kulkarni, A. Watve, M.E. Knight.

Author contributions: CJT Designed and implemented the study and authored the paper: TRL assisted with the study design, data collection, taxonomy and editing; DTB assisted with study design and editing; SK assisted with data collection and logistics; AW assisted with permits and logistics; MEK assisted with study design and editing.

Abstract

Rocky plateaus are globally threatened ecosystems and are frequent landscape features in the northern section of the Indian Western Ghats, globally one of the most important and threatened hotspots. These plateaus are known to support elevated levels of endemic amphibians and flora, but knowledge of their invertebrates is limited. Ants (Formicidae) are environmental sensitive and make excellent biotic surrogates for other taxa. This novel study compared quantitative data for ants and their environment on a representative group of plateaus in western Maharashtra across 2° of latitude and from 67-1179 m elevation we sought to answer, "how were they distributed and what drives that pattern". Climate, season, microhabitats and land-use were investigated. Changes in temperature and rainfall drove macroscale biotic patterns. Locally land-use was highly important in structing very seasonal assemblages. All anthropogenic land-use had a negative impact on some functional groups and wind-turbine installations were favourable for opportunist species. Mutualist relationships with floral phenology was important for seasonal changes together with reducing rainfall and increasing

temperatures. Woody plant and loose rocks were the most important microhabitats. Plateaus were highly individualistic and for conservation purposes should be considered unique, these results are applicable to similar systems in the tropics and sub-tropics.

6.1 Introduction

Ants are a hyper-diverse group occupying almost all biomes and carrying out a wide range of ecological functions (Hölldobler & Wilson, 1990). They can comprise as much as 20% of faunal biomass in forest systems but there have been few studies of the group in the Western Ghats (WG), India, for other ecosystems (Gunawardene, Daniels et al. 2007) but see (Gadagkar et al. 1993; Basu 1997; Gadagkar et al. 2000; Sabu et al. 2008; Anu et al. 2009; Narendra et al. 2011). This is the first published study of the ant assemblages on the rocky plateaus in the northern WG (NWG) but see thesis (Fernandez, 2013; Baidya, 2015). Rocky plateaus in complex landscapes are known to have diverse ant assemblages in South Africa (Munyai & Foord, 2012). Rocky plateaus are of international biodiversity importance, being globally threatened ecosystems with elevated levels of biodiversity and endemism (Porembski et al. 2016). Our knowledge of rocky plateau invertebrate communities in the Western Ghats (WG) and the northern WG (NWG) is limited, in common with much of the tropics (Vineesh et al. 2007; Feeley et al. 2016).

The Western Ghats/Sri Lanka Biodiversity Hotspot is one of the eight most valuable global hotspots and one of the three most threatened (Cincotta, Wisnewski & Engelman, 2000; Myers et al. 2000; Sloan, et al. 2014). The NWG is a geologically and climatically distinct region (see Fig 1.0-1 & 2), characterised by isolated hilltop plateaus formed from ferricretes of laterite in the basalt Deccan Traps volcanic province (Widdowson et al. 1996; Watve, 2013). The plateaus are patchily distributed and likely to function as habitat islands within a topographically heterogeneous landscape, each with an individual environment derived from clines in edaphic conditions, rainfall and temperature (Davidar et al. 2007; Robin et al. 2012; Watve, 2013; Qian et al. 2014). Within each plateau there exists a

complex matrix of microhabitats (Watve, 2013; IMD, 2016; Thorpe et al. 2016). Australian lateritic plateaus have ant assemblages that differ from other ecosystems (Andersen et al. 2010). The ant assemblages on the NWG plateaus may reflect the elevated levels of endemism recorded in other taxa, including plants (Lekhak, 2012), and amphibians (Biju et al. 2009). At a landscape level topography has resulted in population genetic isolation in macaques (Ram et al. 2015) elephants (Vidya et al. 2005) and birds (Robin et al. 2010). The NWG plateaus offer environments with high seasonal contrasts: their scant soil cover over laterite means they are rapidly transformed into seasonal wetlands on the arrival of the monsoon rains (Porembski & Watve, 2005; Watve, 2013). Despite their frequency in western Maharashtra our knowledge of their ecology is limited, although new species are being described regularly from these systems e.g. spiders (Kulkarni, 2014); large Brachiopoda (Rogers and Padhye, 2014); assassin bugs (Kulkarni, 2016); amphibians (Garg & Biju, 2017); reptiles (Giri et al. 2017). There remains an urgent need to better understand the factors structuring the plateau assemblages in the NWG, in order to inform their conservation and management (Sutherland & Wordley, 2017).

6.1.1 Ants and ants as surrogates

Ant distribution changes in a predicable way to their environmental change making them an excellent taxon for spatial comparisons (Yek et al. 2009) and surrogates for wider terrestrial biodiversity including plants, invertebrates and birds (Sauberer et al. 2004). This makes them an ideal focal taxon for studying the comparative ecology of rocky plateaus. Plateau occupancy by ant species is dependent upon a range of temporal, spatial and physical factors including: reacting positively with temperature and rainfall but negatively with temperature and rainfall seasonality (southern WG, review; Anu et al. 2009; Weiser et al. 2010); habitat fragmentation (Austria; Crist 2009); habitat complexity (South Africa, Australia; Gibb and Parr 2013); surrounding habitat (NWG (Fernandez, 2013); temperature (South Africa; Botes et al. 2006)); rainfall (southern WG ; Sabu et al. 2008)); microhabitats (northern India; Bharti et al. 2016 also McGeoch et al. 2011); tree presence and canopy

density (southern WG; Sabu et al. 2008)); anthropogenic disturbance and the presence of tramp or invasive species (NE India ; Bharti et al. 2016) many of which co-vary.

An alternative to directly comparing taxon data, but instead comparing their functional groups, was developed in Australia in the 1990s (Andersen, 1997; King et al. 1998; Andersen, 2000; García-Martínez et al. 2015) and has been applied in India (Vineesh et al. 2007; Narendra et al. 2011; Bharti, 2013). This approach makes use of the differing functional ecology, especially competitiveness, of individual taxa. Both feeding guild and functional group models have been explored with the conclusion that the functional group (FG) model outperformed the feeding guild model and provides a simplified ecological system model sensitive to environmental change (Vineesh, et al. 2007). However, the FG model was developed in Australia where many ecosystems have behaviourally dominant members of the sub-family Dolichoderinae. This has had to be adapted to systems, such as India, where these taxa are either not present or are far less dominant (Narendra et al. 2011).

The study addresses three principal questions:

- How do the ant faunas on the rocky plateaus in the northern WG relate to environmental drivers?
- How are the ant assemblages impacted by anthropogenic disturbance?
- How are plateau ant assemblages affected by seasonal changes?

It compared assemblages across a range of seasonal and spatial scales. Given the global importance of rocky plateaus such studies provide valuable baseline data and information for their conservation in many regions of the globe and in general on island-like terrestrial habitat patches (Adams et al. 2013; Sutherland et al. 2017).

6.2 Materials and methods

6.2.1 Study area and Sampling design

The study area (Fig 1.0-1 & 2) includes the areas both above and below a North-South trending escarpment in the northern section of the Western Ghats/Sri Lanka Biodiversity Hotspot. To assess the spatiotemporal variation in the distribution of surface dwelling ants on the plateaus of western Maharashtra and their environmental drivers, 11 representative plateaus ranging from 67-1179 m above sea level (m) and covering more than 2° of latitude (15.89 to 17.92 °N) were selected to cover most of the distribution of laterite in western Maharashtra. These sites encompass a range of land-uses (Table 6.0-1). For comparative purposes the study area was sub-divided into 2 Regions High and Low, separated by the escarpment. Each was subdivided into three arbitrary latitudinal sections: High North, High Central, High South, Low North, Low Central and Low South.

Rainfall in the NWG is highest along the crest line of the escarpment, with a declining latitudinal pattern in the number of wet days (Hemmings and Andrew, 2017; IMD, 2016; India 2017). Rain is likely on ~11% more days in the south of the study area than the north and 12.7 more frequent above the escarpment (IMD, 2016; India, 2017).

The plateaus of the NWG are under pressure from proximate threats: localised threats such as extraction of non-timber forest products, livestock grazing, and fires, and landscape-level threats such as road construction, hydro power projects, wind farms, intensive agricultural, plantations of exotic species, tourism and open cast bauxite mining (Cincotta, Wisnewski & Engelman, 2000; Phillips, 2012; Lad, 2013; Balaji et al. 2014; CEPF, 2016).

Table 6.0-1. Site descriptions with land use, elevation in m above sea level, land-use, disturbance intensity (Dist. Int.).

Site	Lat	Long	Land use	Dist. Int.	Region	Eco-zone
Chalkewadi	17.5736	73.8261	Wind turbine	Medium	High	High North
Jagmin	17.5927	73.8181	Light	Light	High	High North
Mhavashi	17.4310	73.9313	Wind turbine	Medium	High	High North
Panchgani	17.9217	73.8045	Tourism	High	High	High North
Masai	16.8181	74.0779	Tourism	High	High	High Central
Amboli Low	15.9374	74.0027	Tourism	High	High	High South
Shipole	17.9735	73.0527	Light	Light	Low	Low North
Ratnagiri	16.9627	73.2962	Agriculture	Medium	Low	Low Central
Lanja	16.7419	73.4204	Light	Light	Low	Low Central
Kudopi	16.2327	73.5105	Light	Light	Low	Low South
Dhamapur	16.0315	73.584	Agriculture	Medium	Low	Low South

6.2.2 Sampling methodology

Techniques using standardised protocols which enable comparisons to be made have been developed for surface dwelling, epigaeic, ants, in particular the Ants of the Leaf Litter protocol (ALL) (Agosti, 2000, Bestelmeyer, 2000). However, except for baited sticky paper all these passive techniques require either a substrate that facilitates the insertion of pitfall traps, or the collection of leaf litter. These protocols provide excellent systems to sample many habitats, but they are not suitable for hard substrates such as duricrusts, karst limestone and some urban area surfaces. We developed a novel trapping technique that can be cheaply replicated and used across a range of substrates including hard surfaces. The traps were developed to overcome the challenges of sampling duricrust plateaus in southern India that are a mosaic of micro habitats presenting multiple substrates on a single site with an unknown complex of diurnal, nocturnal and crepuscular species. Sampling needed to encompass areas or soil filled depressions, shallow soil and areas of exposed duricrust without any vegetative cover. The solution was a trap made from a readily available and cheap resource, modified plastic drink bottles with bait (Fig 6.0-1).

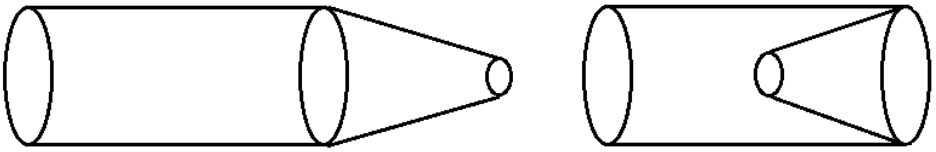


Figure 6.0-1. Conversion of a standard 50 ml plastic drink bottle on the left to a trap on the right. The joint between the two sections is sealed with tape.

Four 100 m survey lines were established on each site incorporating all the available microhabitats. Ten traps were placed horizontally on the ground at equal distances along each survey line baited with 50ml Mirinda™ Pulpy Mango drink and left out for 24 hours. Baits are selective with most attracting dietary generalists, this was deemed acceptable as it will still produce comparable samples (Bestelmeyer, 2000). Trap contents were transferred on site to 70% ethanol in 2 ml plastic tubes. Whilst a single trapping method with single bait introduces sampling bias in this case the bias was accepted as the objective was to obtain comparable samples and not an inventory. In the laboratory the samples were sorted, identified, to the lowest taxonomic level possible, counted and measured. Where identity could not be confidently assigned morpho species identities were used.

6.2.3 Environmental variables

Site latitude, longitude and elevation (m) were recorded using a Garmin Map 60s hand held GPS (Garmin, Olanthe, KS, USA). Eight climate and habitat variables were recorded for each survey line: air and ground temperatures, percentage cloud cover, percentage cloud cover, relative humidity and if it rained during the survey, the percentage area covered by loose rocks, woody plants, exposed rock without soil cover; air and ground temperature.

6.2.4 Data Analysis

Statistical analysis was performed in either Minitab™ v17 (Minitab Inc. USA), Primer-e and Permanova+ (Primer-e Ltd, Plymouth, UK) or PAST (Hammer et al. 2001). Unless otherwise stated

biotic comparisons were made from Bray-Curtis Similarity Matrices of square root transformed data and environmental data from Euclidian Distance Matrices of normalised square root transformed data.

Spatial autocorrelation in environmental and biotic data was assessed through a comparison of Bray-Curtis similarity matrices with an inter-site distance matrix using the RELATE routine in Primer-e v7, with 999 randomised permutations (Legendre, 1993; Legendre et al. 2002).

A series of Permutational Manova's (Permanova) were used for an initial investigation of macro-scale biotic relationships (Jolliffe, 2002; Anderson, et al. 2008). As some spatial units had small numbers of observations, Monte Carlo permutation tests were used to generate a Pseudo *F* statistic and *P* (MC) values, results over a 95% confidence interval are reported. The relative importance of each component in the Permanova was assessed by comparing the square root of the estimates of the components of variation being compared as the % of variation explained (Underwood et al. 1993; Anderson et al. 2008). Seasonality was assessed through comparison of assemblage composition, abundance and species richness.

The impacts of elevation and latitude on total abundance, alpha diversity (taxa number), Inverse Simpson's Index (1-D) and Pielou's J were assessed using Pearson Product Moment or Spearman Rank correlations. Spatial turnover was examined by comparing Whittaker's Beta diversity index (β_w) using the formula: ($\beta_w = \frac{S}{\overline{a}} - 1$) where S = total types in the region and $\overline{a}$ average site sample species diversity (Whittaker 1960; Hammer et al. 2001).

To identify the most important environmental explanatory variables for the ant distribution the BEST BIO ENV routine was performed in Primer-e v7 (Clarke, 2015). This examines all the possible permutations of environmental variables and selects the best and a subset (3 in this case) that

maximises the correlation between similarities of the biotic matrix and the dissimilarities in the environmental matrix (Quinn & Keough, 2002; Clarke & Gorley, 2015). Environmental explanatory power was assessed with non-metric multi-dimensional scaling ordination (nmMDS) of Euclidian Distance matrices of normalised data (Kent, 2012; Clarke et al. 2015).

To assess the impact of anthropogenic land-use on ant assemblages the SIMPER routine was used to generate land-use class similarity percentage values (Clarke et al. 2015) validated with the ANOSIM routine (Clarke et al. 1988; Clarke et al. 2015).

Functional Groups distributions were compared for land-use classes and Regions (Andersen, 2000; Narendra et al. 2011) To compare land use types, a metric multi-dimensional scaling (mMDS) analysis was performed on a rank distance matrix constructed from the ANOSIM R value matrix (Anderson et al. 2008).

6. 3 Results

6.3.1 Distribution patterns in the biota

A total of 10,683 ants were sampled from 11 plateaus sampled on consecutive dates in both the pre- and post-monsoon seasons. The post-monsoon sample in 2013 had the same number of sub-families as the 2014 pre-monsoon sample but fewer individuals (3116:7567), genera (26:30) and taxa (102:109). *Camponotus* was the most specious genera with 21 types in the sample followed by *Crematogaster* and *Monomorium* with 14 each, *Pheidole* had 10 types. The sample was similar to the other 2 plateau ant studies in the NWG both close to the southern edge of the study area: 69% of genera were shared with Fernandez (2013) and 66% of genera and 38% of species with Baidya

(2015). Two morphs possibly with limited distribution were found *Camponotus parius*, golden morph and *Camponotus sericeus*, southern morph both were only found above the escarpment.

6.3.2 Plateau ant phenology

Post-monsoon when seed resources are low the number of samples of granivorous taxa Monomorium and Pheidole were low (13 & 4 respectively) relative to the end of the dry season, pre-monsoon (44 & 26 respectively), as *Monomorium* and *Pheidole* increased types of *Camponotus* decreased, 28 post-monsoon, 21 pre-monsoon.

6.3.3 Invasive and Tramp species distribution

Non-native tramp species and some that are considered invasive, as they are known to displace native species in other ecosystems, were detected at many sites: *Anoplolepis gracilepes* (Smith, 1857) was found on all sites in the Low Region; *Paratrechina longicornis* ssp. (Latreille, 1802) was widely distributed in both Regions but absent from Amboli with a single individual found at Panchgani; *Monomorium pharaonis* (Linnaeus, 1758) was collected on 1 wind turbine site; *Solenopsis geminata* (Fabricius, 1804) was found on 2 Low Region Light Disturbance sites and in the High Region on a site with Tourism and 1 with Wind Turbines.

6.3.4 Spatial patterns in diversity

Site samples varied between Regions and seasons with the High Region sites having lower abundance, species richness (alpha diversity) and diversity (Inverse Simpsons Index) than the Low Region just after the monsoon. However, the High Region had greater site abundance and species richness before the monsoon, but the Low Region still had greater diversity. The negative cline in abundance and alpha diversity was only significant post-monsoon ($\rho = 0.77$, $P<0.01$; $\rho = -0.66$, $P<0.05$ respectively). Combined season gamma was greater in the High Region (115:72). The variation in species composition between sites was greater in the High Region (High Region $\beta_w = 4.4$;

Low Region β_w = 3.4). Inter-regional differences were most marked at species level where out of the ten most abundant taxa only 3 were found in both Regions (Table A.4.1 & 2).

6.3.5 Land-use impact on ant taxonomic distribution

Land-use was the most significant factor influencing the macroscale distribution of taxa explaining 40% of the variation in the sample with Latitude 21% and elevation 14%. Land-use was nested within latitude and elevation. Ant taxonomic composition varied between land use classes (Table A.4.2).

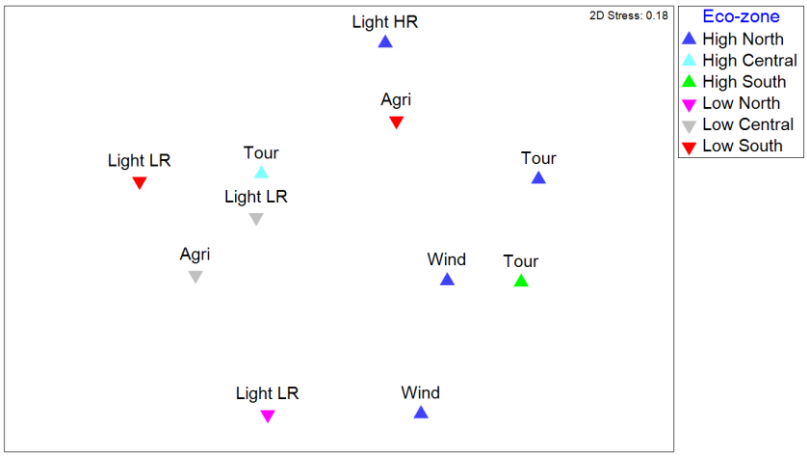


Figure 6.0-2. nmMDS ordination of biotic data pooled from 2013 post monsoon and 2014 pre-monsoon surveys and illustrated by land-use and Eco-zone. Annotated for land-use: Agri-agriculture; Light HR-light disturbance in High Region above the escarpment; Light LR-light disturbance in Low Region below the escarpment; Tour-tourism; Wind-wind turbine installations.

The nmMDS ordination shows the Regions are distinct with the High Region sites more dispersed then the Low Regions sites centre left cluster (Fig 6.0-2). Within those clusters land-use has an impact with Tourism in the High Region appearing to have the greatest impact: Panchgani and Amboli close together despite being geographically wide apart (217 km) with their data points about the same distance from each other as the two Wind Turbine sites which are only 25 km from each other. The High Region site Masai (top right) with tourism was very dissimilar to the other tourism sites possibly due to climatic conditions as it is further to the east away from the crest line of the escarpment and

presumed to be drier, possibly with similar rainfall to the Low Region plateaus it is placed adjacent to. The SIMPER routine in Primer-e was used to refine the analysis of the impact of land-use finding that greater dissimilarity between land-use pairs than within land-use classes. The sites in the Tourism class were more like each other than the pair of Wind Turbine sites reinforcing the nmMDS result that land-use has the greatest impact. ANOSIM analysis validated the findings ($R=0.524$, $P<0.05$) with one refinement, in the Low Region within class variation was higher than between classes ($R= -0.417$, Significance 100%).

Ant assemblages varied between land-use classes (Table A.4.2). The abiotic drivers of those distributions were further investigated in the BEST BIO ENV (Primer-e v7) routine which found seasonal differences between the drivers. Post-monsoon habitats were most important but pre-monsoon the drivers were entirely climatic.

6.3.6 Patterns in the distribution of functional groups

Macroscale distribution of functional groups was even in most groups except there were more Generalised Myrmicinae and Subordinate Camponotini in both Regions (Fig 6.0-3). Only 2 types Specialist Predators were found Pre-monsoon on Masai where disturbance comes from a combination of tourism and grazing, Post-monsoon only 1 was found on Jagmin the Light Disturbance site in the High Region. Due to this low frequency they are not illustrated in the figures.

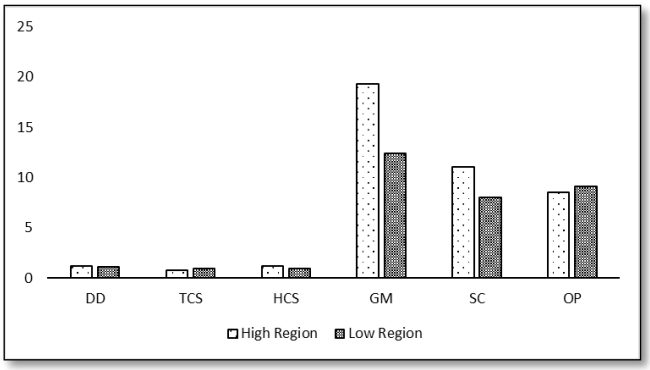
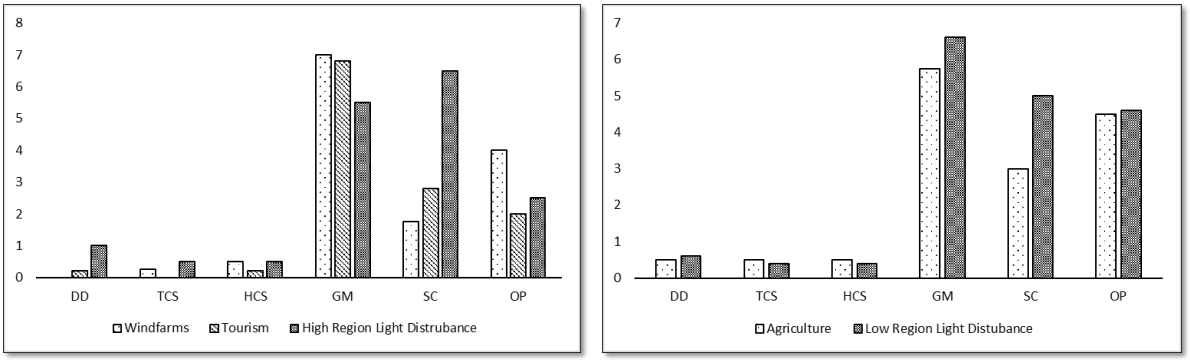


Figure 6.0-3. Distribution of functional groups between Regions above (High Region) and below (Low Region) the escarpment. DD-Dominant Dolichoderini; TCS-Tropical Climate Specialists; HCS-Hot Climate Specialists; GM-Generalised Myrmicinae; SC-Subordinate Camponotini; OP-Opportunist species.

The impact of land-use is seen in the reduction of Dominant Dolichorerini from sites with wind turbines and tourism compared to light disturbance reference sites (Fig. 6.4a). Tropical Climate Specialists were absent from tourism sites and Hot Climate Specialists had lower frequency, wind turbine installations had less impact on the group (Fig 6.0-4a). Generalised Myrmicinae appear to be much more tolerant of wind turbine installations and tourism compared to Subordinate Camponotini (Fig 6.0-4a). With wind turbine installations having the greater impact an effect underlined by the increase in Opportunists (Fig 6.0-4a). In the Low Region agricultural disturbance has had a similar impact with the proportion of Subordinate Camponotini relative to Generalised Myrmicinae decreasing with both being lower than on the Light Disturbance sites (Fig 6.0-4b). Agriculture did not have an impact of the occurrence of Opportunist, Specialist or Dominant Dolichoderini (Fig 6.0-4b).



a) b)

Figure 6.0-4a & b. Relative proportions of the functional groups, corrected for sampling bias, by land-use classes and divided into the two Regions. High Region above the escarpment, Fig 24a with Low Region as Fig 24b. DD-Dominant Dolichoderini; TCS-Tropical Climate Specialists; HCS-Hot Climate Specialists; GM-Generalised Myrmicinae; SC-Subordinate Camponotini; OP-Opportunist species.

6.3.7 Spatial structuring in the environment

Both air and ground temperatures declined with elevation (ρ = -0.53, P<0.05; ρ = -0.56, P=0.08 respectively) as did the abundance of woody plants (ρ = -0.66, P<0.05). Pre-monsoon cloud cover declined with latitude (ρ = -0.64, P<0.05). Post-monsoon ground and air temperatures declined with latitude (ρ = -0.6, P=0.07; ρ = -0.78, P<0.01 respectively). Inter-regional temperature ranges vary with Low Region range of 25° compared to the High Regions 38°C. There were no significant patterns in the distribution of other climatic or habitat variables with, season, elevation or latitude. The spatial pattern of site distribution in the nmMDS ordinations did not follow latitude and elevation but did separate the sites below and above the escarpment (Fig. 6.0-5).

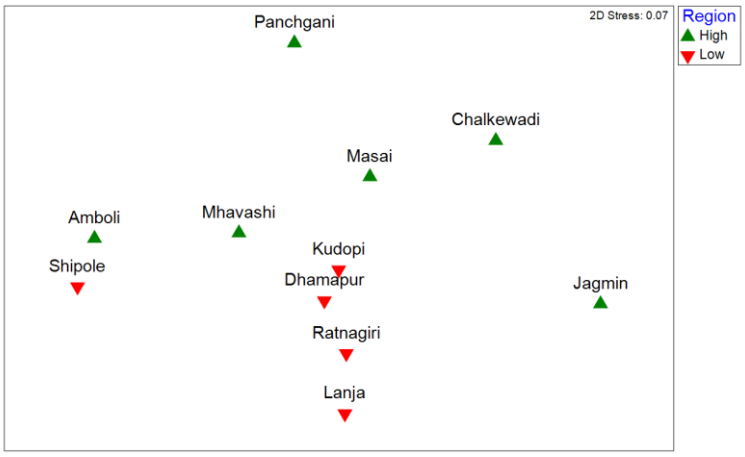


Figure 6.0-5. nmMDS ordination of normalised environmental data from combined pre and post monsoon surveys. Region: High-above the escarpment; Low-below the escarpment.

The pre- and post-monsoon environmental data showed plateau environment above the escarpment was more variable than in the coastal area.

6.4 Discussion

The distribution of ants on the rocky plateaus in western Maharashtra was not random at all levels of organisation and all spatial and temporal scales. Abiotic changes linked to elevation and latitude were

the principal drivers of the spatiotemporal patterns at a macroscale, but land-use influenced local structuring. Rainfall frequency depressed ant activity in both seasons. During the post-monsoon season habitats and food resources were important in the BEST BIO ENV analysis, loose rocks and woody plants. Before the monsoon climatic parameters were more significant in the BEST BIO ENV analysis in structuring assemblages with temperature, rainfall frequency and cloud cover being most important. There were four invasive/tramp species found but these do not appear to have had the expected negative impact on communities one (*Anoplolepis gracilepes*) was restricted to sites below the escarpment. Land-use structured both taxonomic and functional group assemblages. Intra-land-use class assemblages were more similar then between class comparisons. Of the anthropogenic land-use types wind turbine installations and tourism had the greatest impact on ant assemblage composition.

6.4.1 Seasonality in the northern Western Ghats changes ant abundance and richness

Ant populations on NWG plateaus were at their lowest in species richness and abundance at the end on the monsoon reflecting the sensitivity of many taxa to rainfall and low temperatures (Basu, 1997, Anu, et al. 2009). Alpha diversity and abundance increased as the dry season progressed on High Region plateaus, reflecting similar observations from the southern WG (Anu et al. 2009) and NWG south of this study (Fernandez, 2013; Baidya, 2015). Below the escarpment, where rainfall is lower and there are fewer days with rain, the seasonal difference was almost imperceptible.

Predictably, as the dry season progresses NWG plateau ant assemblages continued to change in line with energy availability but also reflecting changing resource availability for some taxa (Fernandez 2013; Baidya 2015). Ant distribution is known to be strongly correlated with floral communities (McGeoch, et al. 2011). Evidence for a phenological link between plant and ant assemblages was proposed by Baidya (2015). The plateau plant community is highly seasonal dominated by ephemeral flush vegetation and resurrection plants which grow during the monsoon and flower and seed at the

end of the rains (Porembski & Watve, 2005, Watve, 2013). Both Baidya (2015) and this study found an increase in granivorous taxa, such as *Phieldole* sp. and *Monomorium* sp., as seed resources increase. He reports their maximum around the middle of the dry season, but we suggest it is likely the progression is longer. Fernandez (2013) showed three different dry seasonal periods with Baidya's (2015) investigating the early and mid-season and this study the early and late seasons. Baidya (2015) reported granivores were replaced by species like *Camponotus sericeus* as the dry season progressed but this study found a 25% reduction in *Camponotus* sp. A likely conclusion is the assemblage develops continuously during the dry season as available energy increases, rainfall decreases and resource availability changes.

6.4.2 Spatial structuring in the environment drives macroscale ant distribution

Rainfall and temperature change with topography as well as between seasons in the study area. The study supports the view that temperature and rainfall act synergistically in driving macroscale ant distribution with other land-use, microhabitat and resource availability key at a local scale (Jenkins et al. 2011, Szewczyk &McCain, 2016). This helps to explain the elevational reduction in ant species richness as temperature decreases and rainfall increases with elevation in the study area (Hölldobler & Wilson, 1990; Kaspari et al. 2000); Szewczyk & McCain, 2016). Other studies in the southern WG found abundance and species richness (Shannon Index) peaked at ~1000 m, but with inter sub-family variation (Sabu et al. 2008) and in the north of India both species and generic richness peaking at ~1000 m (Bharti, 2013). Notably, most inter-plateau differences occurred at assemblage level suggesting the ecological requirements of individual taxa drive the larger scale pattern. A potential explanation of the difference from this study is the extreme nature of plateau climates on isolated sites above the escarpment which is unlike forest of grassland ecosystems. Such a model would explain the elevational increase in inter-site diversity. It would concur with the elevational band model of (Bharti, 2008) and the distribution of favourable climate and habitat described by Sabu et al. (2008).

Elevated temperatures below the escarpment may be a selective factor in ant assemblages despite the general view that higher temperatures are associated with greater ant abundance and richness (Kaspari et al. 2000, Gibb et al. 2015). On low elevation plateaus temperature peaked at 45.1°C with a mean ground temperature of 34.9°C with Watve (2011) reports plateau daytime surface temperatures ~50°C. Perhaps favouring climate specialist taxa such as the Tropical Climate Specialist *Oecophyla smaragdina* (Fabricius, 1775) found only on Low Region sites. The optimal fitness range in tropical insects (at 6°N) is much narrower than in their temperate counterparts peaking at ~28°C (Deutsch, et al. 2008). Such temperatures may exceed ant optimum foraging temperatures of 32.3 - 40.6°C (Hölldobler & Wilson, 1990; Kaspari et al. 2000). However, behavioural mechanisms may enable the avoidance of extremes by accessing suitable microclimates which may be associated with microhabitats (Kaspari et al. 2000) the availability of suitable microhabitats may determine distribution (Hemmings & Andrew, 2017). Refugia such as woody plants and loose rocks were found to be important and as the seasonal temperature increases they become the most crucial factor in distribution.

Inter-site climate variability resulting from topographical heterogeneity may impact on both dispersal ability and the creation of complex thermal niches possibly driving the High Region gamma diversity (Janzen, 1967; Ghalambor et al. 2006; Archibald et al. 2013; IMD 2016; India 2017). Inter-season variability in alpha diversity in the Low Region was smaller than above the escarpment reflecting the more even temperature and lower rainfall (Hobbhahn et al. 2006; Watve, 2010).

6.4.3 Impact of climate change on plateau ant assemblages

The Intergovernmental Panel on Climate Change (IPCC) predict future temperature increases and less reliable monsoon rains in southwest India (IPCC, 2014). Future temperature increases may be an issue for some NWG ants where the species physiological adaptive limits are possibly close to their environmental maxima (Pereira et al. 2017), tropical invertebrates having a lower tolerance to warming and a narrower thermal safety margin (Deutsch et al. 2008). Climate change will impact the

vegetation and by association impact the ant assemblages. Lowland tropical biotas, such as those in the Konkan, are predicted to suffer the greatest attrition through temperature increases (Colwell et al. 2008). Many study species are likely obligate mutualists associated with specific plants and changes in phenology will impact the ant species (Botes et al. 2006).

6.4.4 The role of microhabitats in ant distribution

Woody plants and loose rocks were the most important regulatory microhabitats in the analysis they may provide a range of ecological resources on and around plateaus. Woody plant composition was found to be more important than the herbaceous or ground plants in an Australian lateritic plateau study (Andersen et al. 2010). Woody plants add structural complexity to rocky plateaus, as do loose rocks, and habitat complexity drives ant diversity (Lassau & Hochuli, 2004, Gibb & Parr, 2010). The woody plants were not uniformly distributed with their percentage cover declining with elevation. That would be one explanation for higher diversity in the Low Region. In addition, plateaus with escarpment rather than forest edges were more common at higher elevations. Fernandez (2013) found plateau assemblages highly like the surrounding forest it seems plausible that woody plants both on and adjacent to the plateaus were important structuring factors in source-sink dynamics for meta-population species (Hanski, 1998, Hanski,2015).

6.4.5 Land-use structures ant functional groups at a local scale

Functional Group (FG) ecology is still in it's infancy in the WG where knowledge of individual species ecology is limited (Vineesh et al. 2007). The framework described in (Andersen, 2000) was used but with reference to (Vineesh et al. 2007, Narendra et al. 2011). Generalised Myrmicinae were the most abundant FG followed by Subordinate Camponotini in both Regions (Andersen, 2000). The impact of anthropogenic disturbance in the form of land-use was not uniform possibly because disturbance interacts with temperature and rainfall (Gibb et al. 2015). Unlike the High Region sites those in the Low Region had greater intra-class variability than inter-class suggesting a more even

distribution with light agricultural land-use having a minor impact. Above the escarpment Generalised Myrmicinae were not impacted by either wind turbine installations or tourism but Subordinate Camponotini were, more severely by wind turbines. The ecological space left open by the reduction in ant diversity on the wind turbines sites allowed Opportunists space to establish. Below the escarpment the low intensity agriculture reduced both Generalised Myrmicinae and Subordinate Camponotini resulting in a slight increase in Opportunists compared to light disturbance sites. The study supports (King, et al. 1998) in that the frequency of Dominant Dolichorinae was reduced by all anthropogenic land-uses. They go on to say Tropical Climate Specialists are intolerant of disturbance, this study supports that for tourism and wind turbine installations but not low intensity agriculture.

6.5 Conclusion

Rocky plateau ant assemblages in the northern Western Ghats are highly individual but with core similarities. Their distribution is the result of multiple drivers whose individual impact operates at a range of spatiotemporal scales. At a macroscale, rainfall and temperature structure regional and seasonal assemblages. Within individual plateaus land-use, spatial heterogeneity and floral diversity is important. Anthropogenic land-use in particular the installation of wind turbines and then tourism have negative impacts on plateau ants by excluding some species. It is likely that several species are obligate mutualists dependent upon unidentified plant species. Changes in rainfall patterns are likely to negatively impact ant assemblages. Increases in temperature may negatively affect ant taxa especially those restricted to the low lying coastal area. Ants as a group make excellent surrogate taxa for assessing change both natural and anthropogenic, on the rocky plateaus in the NWG. For conservation purposes each plateau, especially those above the escarpment, should be considered unique. Land-use change should be carefully monitored.

Chapter 7. Spatiotemporal cross taxa congruence in an archipelago of sub-tropical rocky terrestrial islands, Western Ghats, India.

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Author contributions: CJT Designed and implemented the study and authored the paper: TRL assisted with the study design, data collection, taxonomy and editing; SK assisted with fieldwork and logistics; DTB assisted with study design, taxonomy and editing; AW assisted with permits and fieldwork; MEK assisted with study design and editing.

Abstract

Rocky plateau biota has elevated levels of biodiversity and endemism and are internationally threatened ecosystems. The study investigated spatiotemporal structuring and cross-taxon congruence in three surrogate taxa on the sub-tropical rocky plateaus in the northern Western Ghats, India. Ant, amphibian and aquatic Coleoptera assemblages were compared from a representative group of rocky plateaus in the north of the Western Ghats/Sri Lanka Biodiversity Hotspot. These taxa represent fully aquatic, semi-aquatic and terrestrial ecologies and could be used to detect seasonal differences as well as spatial. Rocky plateaus are internationally threatened ecosystems and those in the northern Western Ghats are recognised as vulnerable from anthropogenic activity. Study sites extended over 2 degrees of latitude and 67-1200 m elevation. The use of biotic surrogates can be useful to identify conservation priorities in the absence of adequate time or funds to carry out biodiversity inventories. All three groups were good surrogates of macroscale spatial climatic differences and for localised

impacts resulting from tourism and wind turbine installations. Community similarity comparisons provided better results than more traditional richness correlations in these taxa. Water beetles then ants proved the best surrogates for the other taxa. We conclude the plateaus above and below the escarpment are highly individualistic and are impacted by anthropogenic land-uses and are worthy of careful assessment prior to any land use change.

7.1 Introduction

Rocky plateaus are globally threatened ecosystems at the same time they are known to have elevated levels biodiversity and endemic species (Jocque et al. 2010; Porembski et al. 2016). Those in the northern section (NWG) of the Western Ghats-Sri Lanka Biodiversity Hotspot (WG) are unique in India and face multiple stressors (Fig 1.0-1, 2 & 4 [Widdowson & Cox, 1996; Watve, 2013; IMD, 2016; Thorpe & Watve, 2016]). Therefore, there is an urgent need to assess their ecological importance and conservation value. This would ideally require exhaustive inventories of their biodiversity to enable informed conservation priorities to be set (Chettri, 2010; Sutherland & Wordley, 2017). Due to constraints in logistics, time and money always make this an unviable option (Chettri, 2010). Typically, instead, biological or environmental surrogates are selected to overall biodiversity or environment (McGeoch, 1998; Bilton et al. 2006; McGeoch et al. 2011). In the NWG, along with many other sub-tropical regions, this is hampered by a shortage of information on suitable surrogate taxa but see (Prasad et al. 1998; Das et al. 2006).

The WG are a 1500 km long chain of hills rising from the coastal littoral along the southwest coast of India. They are bounded on their western edge by a 500 m high erosional escarpment separating them from the coastal area, the Konkan (Fig 1.0-4 [Widdowson & Cox, 1996]). Elevation ranges from sea level to ~1200 m above sea level (m) with variation in elevation is much less evident in the Konkan (Watve, 2013). The WG are biologically separated into three by two breaks in the hills forming south, central and north (NWG). Gene flow is restricted across these breaks in: elephants (Vidya et al. 2005);

macaque monkeys (Ram et al. 2015); birds (Robin et al. 2010) and amphibians (Van Bocxlaer et al. 2012). At a finer scale genus level genetic differentiation is recorded in birds between hilltops in the southern/central WG (Robin et al. 2017) and toad genera in the northern Western Ghats (Biju et al. 2009).

NWG lateritic rocky plateaus form important isolated landscape elements in the WG, one of the eight most important biodiversity hotspots (Vidya et al. 2005; Biju et al. 2009; Lekhak, 2012; Robin and Nandini, 2012; Kasturirangan et al. 2013; Sloan, et al. 2014). They are irreplaceable landscape elements in a vulnerable region (Brooks et al. 2006; Bharucha, 2010; Kasturirangan et al. 2013; (Watve, 2013). Further the WG are one of three hotspots most threatened by population growth (Cincotta, Wisnewski & Engelman, 2000). NWG rocky plateaus are complex mosaics of microhabitats known to have diverse flora and fauna with high rates of endemism in plants, invertebrates and amphibians (Lekhak, 2012, Munyai & Foord, 2012, Watve, 2013; Giri, 2016, Thorpe & Watve, 2016). They are under pressure from a range of anthropogenic activities: livestock grazing, fires, road construction, hydro power projects, wind farms, intensive agriculture, introduction of exotic species, tourism, open cast bauxite mining and disease (Cincotta, Wisnewski & Engelman, 2000; Phillips, 2012; Lad, 2013; Balaji et al. 2014; CEPF, 2016; Thorpe et al. 2018).

Although the practice of employing biological surrogates is widespread, there are challenges to the theory, with the validity of the results relying upon good congruence between the taxa of interest and the chosen surrogate (McGeoch, 1998; Heino, 2010; Qian, 2010). There is little data on surrogacy in the sub-tropics and even less information on cross seasonal congruence and none specific to the NWG. Bio-indicators can be used to answer question relating to: the environment, ecology and biodiversity (McGeoch, 1998) each requires a different methodology, but all need a suitable bio-indicator assessed over an appropriate spatiotemporal. Bio-indicators have historically been selected based on ease of monitoring, detection, identification and well understood ecology (Heino, 2010).

Frequently, comparisons are made between species richness and diversity, although this has been questioned as it fails to capture shifts in community assemblages which may occur with same levels of richness and diversity (Su et al. 2004; Bilton et al. 2006; Roque et al. 2017). Differing factors structure assemblages at varying spatial scales, for example abiotic factors such as climate are important at large spatial extents being replaced by species ecology, biotic interactions (Hortal et al. 2010) and anthropogenic disturbance (Lundkvist, 2002; Newbold et al. 2014).

Care needs to be exercised in sampling design in topographically heterogenous landscapes such as the NWG where complex localised climates may restrict species dispersal and distribution (Ghalambor et al. 2006; Rodríguez et al. 2015). In these areas of complex terrain changes in taxa with high site fidelity and low dispersal ability may only be detected at larger spatial extents, for example amphibians (Schwarzkopf & Alford, 2002; Rodríguez et al. 2015).

The rocky plateaus in the NWG with their relatively simple, but highly seasonal, ecology may serve as model systems in comparative studies of change. Inselbergs have been proposed as model systems and the NWG rocky plateaus, especially those above the WG escarpment, are ecologically similar to inselbergs (Barthlott, 2000). Pools within rocky environments have also been proposed as model systems for similar reasons of simplicity, isolation and accessible taxa (De Meester et al. 2005; Brendonck, 2010). Suitable bio-indicators in such systems include aquatic coleoptera (Bilton, et al. 2006), ants (Munyai & Foord, 2012; Munyai & Foord, 2015) and amphibians (Loyola et al. 2007). Using rarity, endemism rates and species richness Das et al. (2006) in their WG study did not identify either a habitat or taxa that represented all others, although amphibian richness was a surrogate for threatened and endemic species richness. It is possible there were community changes in the areas they investigated but in community profiles rather than their chosen metrics. Comparisons of taxon assemblage comparisons have been proposed as the better metric for spatial comparisons (Bilton et al. 2006).

Temporal factors such as season can change assemblages as species ecology determines their presence for example because of resource availability (Baidya, 2015) or dispersal (Bilton, 2014; Rodríguez et al. 2015) or detectability (Tulloch et al. 2016). Such seasonal shifts may be best assessed through temporally comparable assemblage comparisons (Basu 1997; Su et al. 2004; Rossi & Blanchart, 2005).

There is a growing recognition that better evidence is needed to make sound conservation decisions (Adams & Sandbrook, 2013; Sutherland & Wordley, 2017). Sub-tropical heterogenous environments in biodiverse regions such as the WG are under-represented in the literature for surrogates and cross taxon congruence (Schuldt et al. 2015). In the face of the urgent need to assess and prioritise rocky plateaus in the NWG for conservation the study investigated possible surrogate taxa (Pawar, 2007; Chettri, 2010). The focal taxa were carefully selected to reflect different resource uses spread across both habitat and time, including fully aquatic, semi-aquatic and terrestrial taxa. Amphibians in the NWG include species that are fully aquatic but also species that are substantially terrestrial and caecilians that are semi-fossorial. Lentic Coleoptera are obligate aquatic taxa. Plateau surface dwelling ants are terrestrial and include arboreal species.

As more work has been done on NWG plateau plants we addressed rocky plateau faunal cross taxon congruence to answer two principal questions using three carefully selected taxa to give the ecosystems first overall biodiversity assessment:

- How does individual plateau biodiversity/taxon assemblages vary between the plateaus in the NWG?
- What are the drivers of the differences?
- What are the relative roles of the environment along clines in elevation, latitude and disturbance?

- Are any patterns in distribution and drivers consistent across all the focal taxa?'
- The questions will be examined inter and intra-plateau and at a range of spatial scales.

At the same time as answering the main questions comparisons were made between species richness, diversity and community composition for communities of aquatic Coleoptera (Coleoptera), ants and amphibians found on the rocky plateaus in western Maharashtra, India. To find if there is a single taxonomic group that represents inter-plateau biodiversity?

7.2 Methods

7.2.1 Study area and Sampling design

The study area (Fig. 1.0-1 & 2) incorporates the areas either side of the North-South trending escarpment in western Maharashtra in the northern section of the Western Ghats/Sri Lanka Biodiversity Hotspot. To assess the spatiotemporal variation in the three focal taxa 13 representative plateaus ranging from 67-1179 m above sea level (m) and covering more than 2° of latitude (15.89-17.92 °N) were assessed, covering most of the distribution of laterite in western Maharashtra. The study area encompasses a range of land-uses (Fig. 1.0-1 & 2; Table 1.0-3). For comparison the study area was sub-divided into 2 Regions, High and Low, above and below the escarpment and these were subdivided into three arbitrary latitudinal sections. Identified as: High North, High Central, High South, Low North, Low Central and Low South.

Within the study area rainfall increases up the escarpment and decreases with latitude as rainfall seasonality increases (Hemmings & Andrew, 2017; IMD, 2016; India, 2017). There are around ~11% more days with rain in the south of the study area than the north and rainfall is 12.7 more frequent above the escarpment (IMD, 2016; India,, 2017).

7.2.2 Sampling methodology and taxon identification

Sites were selected to include as many land-uses in each area as practicable; these included light disturbance sites above and below the escarpment, agriculture, wind turbine installations and tourism. Standardised protocols were used to sample the focal taxon from each of the 13 survey sites. Ants were collected using a novel baited trap with 10 traps placed along 4 x 100 m survey lines laid out on each plateau to incorporate all available microhabitats. Collections were made just after and just before the monsoon in 2013-2014 making a total of 80 trap events per site. Amphibians and Coleoptera were sampled on the same sequential survey days and they were in similar weeks each year. Coleoptera were sampled from six vernal pools on each of the same plateaus as the ants and amphibians in 2012, 2013 and 2014, test sites from 2012 were dropped from future surveys. Sampling was standardised by time and included searching all the available microhabitats within each pool. Amphibians were detected using visual encounter surveys with additional refugia searches along 4 belt transects each 100 x 6 m in 2013 and 2014. Transects were placed to encompass as many microhabitats as possible. Individuals were identified on site or photographed for later identification. Ants and Coleoptera were sorted, counted and identified later in the laboratory to the lowest taxonomic level possible. For full details of sampling methodologies please see thesis Chapter 2 for Coleoptera, Chapter 3 for Amphibians and Chapter 6 for Ants.

7.2.3 Data Analysis

Abundance data sets for each focal taxon were created as Excel worksheets with those data combined to create an All Taxa data set for comparison and analysis. Spatial autocorrelation in all data sets was assessed by comparing Bray-Curtis similarity matrices with an inter-site distance matrix using RELATE (Primer-e v7) with 999 randomised permutations (Legendre 1993; Legendre, et al. 2002).

Spearman rank correlations were used to test for between taxa correlations in abundance, alpha diversity, species richness and community evenness in Minitab™ v17 (Minitab Inc., USA). Cross taxon community similarity was compared and related to spatial distribution and land use in Primer-e

v7 (Plymouth Routines in Multivariate Ecological Research, version 7; Clarke & Gorley, 2015). All data sets were square root transformed before Bray-Curtis similarity matrices were calculated. Non-metric multidimensional scaling (nmMDS) plots were visually compared for spatial and land-use responses for each taxon.

Statistical comparisons of the correlation between individual taxa responses to the spatiotemporal environment were made through 'Second stage' MDS analyses (Primer-e v7; Clarke, et al. 2006). The analysis compares similarities between the first stage MDS ordinations of each taxa by creating a matrix of pairwise Spearman rank correlations (ρ). An MDS plot was then produced from the ρ matrix. This 'second stage' MDS can be considered as an MDS of MDSs and illustrates by proportional separation of data points the relationships between each taxa. Assemblages with closer data points being more similar than those with wider spaced data points.

Nonparametric RELATE tests, a form of MANTEL test, were performed in Primer-e to assess cross-taxon congruence and to correlate individual taxa (Clarke, 2015). The tests were performed using Spearman Rank correlations with 999 permutations of individual taxa matrices. Each matrix was based upon individual taxa community abundance data except for ants where both pre and post-monsoon data sets were used together with a combined survey data set. Data were square root transformed before a Bray-Curtis similarity matrix was calculated.

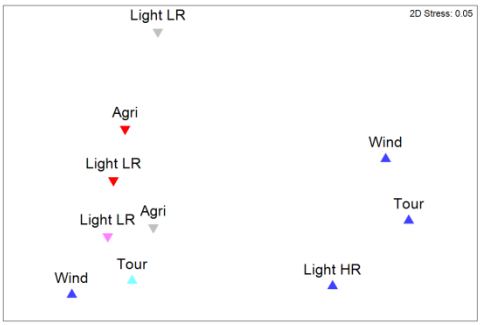
7.3 Results

The diurnal amphibian surveys for 2013 and 2014 combined produced a sample of 276 individuals representing 2 orders, 6 families and 21 species. Pre- and post-monsoon ant surveys produced a sample of 10,683 individuals (Table 7.0-1). The post-monsoon sample in 2013 had the same number of sub-families as the 2014 pre-monsoon sample but fewer individuals, genera and taxa (Table 7.1). The total of 915 individual beetles collected across three years comprised 44 taxa from five families.

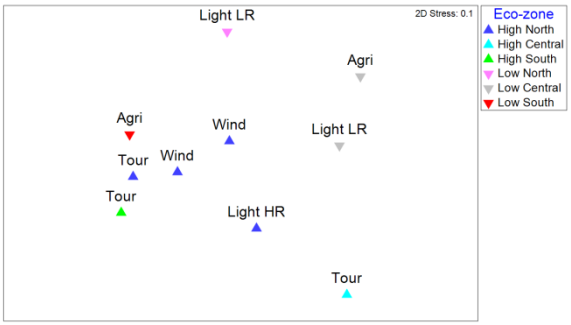
Table 7.0-1. Taxonomic summary for each of the focal groups with totals for the number of individuals in the sample and a summary of types in each classification class. Ant data refers to sub-families Amphibians and Coleoptera to Family. Post-Post monsoon survey, Pre-Pre-monsoon survey.

Taxon	Sample	Abundance	Order	Sub/Family	Genera	Taxa
Amphibians	2013-2014	276	2	6	15	21
Ants	2013 Post	3116	1	5	26	102
Ants	2014 Pre	7567	1	5	30	109
Coleoptera	2012-2014	915	1	5	27	44

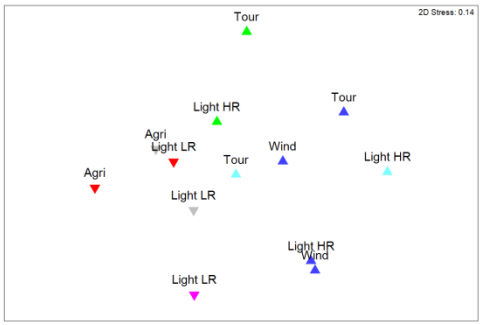
Amphibians were the richest taxa at all three higher taxonomic levels, Order, Family and genera if the ratio of genera to type is compared (Table 7.0-1). In comparing inter-taxa correlations in abundance, alpha diversity, species richness and community evenness only post-monsoon ant and Coleoptera species richness (Shannon Weiner H') were related ($\rho = 0.842$, $p < 0.01$).



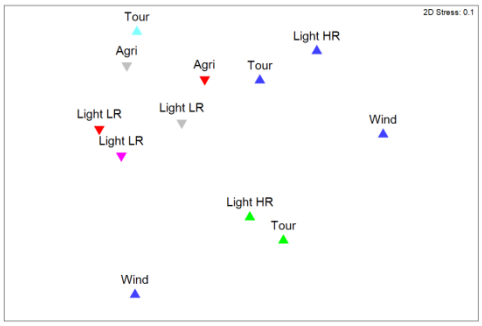
a)



b)



c)



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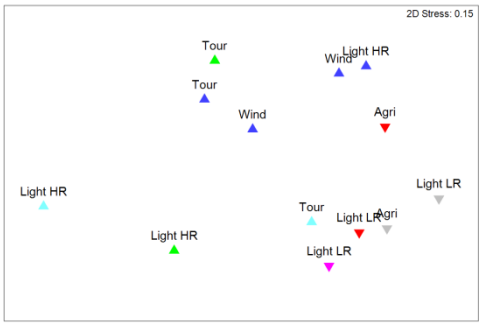

e)

Figure 7.0-1a-e. Non-metric multi-dimensional scaling (nmMDS) of sites based on Bray-Curtis similarity matrices of square root transformed abundance data for individual and combined taxa. High Region sites are denoted by upward pointing triangles and Low Region sites by downward pointing triangles, all are coloured denoting Eco-zones. Site Eco-zone are described in the legend in b) which applies to all MDS plots. The proximity of the data points is proportional to their assemblage similarity i.e. the closer the points the more similar they are. Plot: a) Ants 2013 Post-monsoon; b) Ants 2014 Pre-monsoon; c) Coleoptera; d) Amphibians; e) All taxa combined. Land-use types: Agri-agriculture; Light HR-low disturbance plateau in the High Region (above the escarpment); Light LR-low disturbance plateau in the Low Region (below the escarpment); Tour-tourism; Wind-wind turbine installations. Distance between data points is proportional to assemblage similarities i.e. sites with points that are closer together are more similar than those spaced widely apart.

The two Regions of the study area, High and Low, are distinct in all the MDS ordinations for all three taxa suggesting spatial congruence at a macroscale (Fig 7.0-1a-d). All taxa indicate that the High Region is more heterogenous in assemblages. The agreement between taxa for the impact of land use is less clear and in the Low Region neither the impact of latitude or land use is obvious (Fig 7.0-1a-d).

All the MDS plots separate the plateaus from above and below escarpment (Fig 7.0-1a-e). None consistently place all sites in latitudinal order. The post-monsoon ant diversity was similar in species richness to that of the Coleoptera and both support spatial distribution patterns with limited influence from different land-uses (Fig 7.0-1a & c). The Coleoptera and amphibians were most sensitive to macro-spatial differences (Fig 7.0-1c & d). Pre-monsoon ants were most sensitive to land use indication both tourism and wind turbine installations and rainfall indicated by the separation of Masai a High Centre site located away from the escarpment and thus dryer (Fig 7.0-1b). In most ordinations it is placed closer to the Low Region sites which have similar rainfall. The pre-monsoon ant diversity is most sensitive to tourism as a land-use placing the two tourism site data points close to one another despite their being at opposite ends of the survey area (Fig 7.0-1b). They also indicated light disturbance in the centre and south above the escarpment had similar diversity and separated the High North light disturbance site from the wind turbine sites despite one being adjacent to it geographically (Fig 7.0-1b).

There is limited topographical heterogeneity below the escarpment where a latitudinal signal may be expected but except for Coleoptera and combined taxa there is no consistent signal (Table 7.0-1c & e). There is some indication that amphibians were impacted by agriculture (Table 7.0-1d).

Combining all three taxa improves focus with clear separation of both land use and spatial distribution (Fig. 7.0-1e). The data points for the two High Region sites with tourism are placed close together despite being at opposite ends of the survey area. The High North sites are placed close to each other.

The Low Region sites are clustered in the top right of the plot. Two of the three light disturbance sites in the High Region are separated from the others.

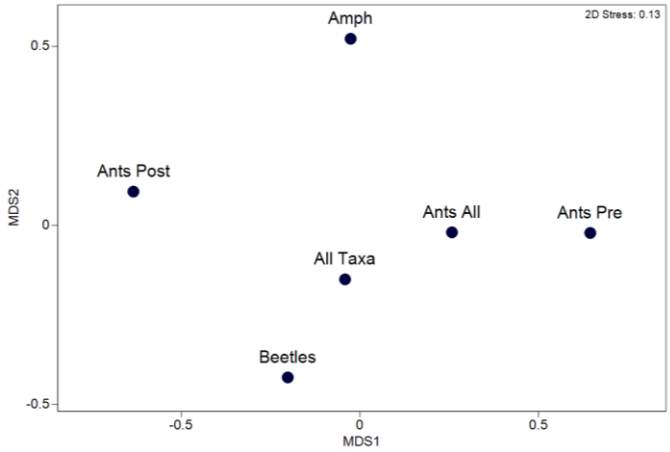

Figure 7.0-2. 2nd stage MDS plot of ρ values from Spearman Rank correlation pairwise comparisons of the individual taxa nmMDS ordinations. Data points are labelled for their taxa: Amph-Amphibians; Ants Pre- is ant data from 2014 Pre-monsoon survey; Ants All- is both ant surveys combined; Ants Post-is ant data from 2013 Post-monsoon survey; All Taxa- is the data set for all taxa groups combined; Beetles-water beetles.

The second stage MDS (Fig 7.0-2; Table 7.0-2) indicates water beetles are the best surrogates for the three taxon groups. The result is reinforced by the Spearman rank correlation values from the MDS matrix (Table 7.0-2). As it was the only group with a Rho value (90) exceeding that needed to justify their use as surrogates for the other taxa, using the published threshold of $\rho > 0.75$ (Table 7.0-2 [Lovell et al. 2007]).

Table 7.0-2. Spearman rank correlation Rho values from 2nd stage MDS analysis of single taxon MDS matrices with each taxon compared to the All Taxa matrix.

	All Taxa
Ants Post-monsoon	0.31
Ants Pre-monsoon	0.31
Ants both seasons combined	0.67
Coleoptera	0.78
Amphibians	0.44

The RELATE analysis supported the MDS ordination but with the water beetles were the second best surrogate of all the taxa data behind combined ant survey data (Table 29) supporting, but not

mirroring, the 2nd stage MDS result (Table 7.0-2 & 3). Both individual ant surveys and amphibians had moderate positive significant relationships with the all taxa data (Table 7.0-3). Amphibians had a moderate positive near significant (P=0.06) association with the all taxa data set (Table 7.0-3). The pre-monsoon ant survey best represented the combined ant data set (Table 7.0-3). Water beetles had weak significant relationships with amphibians and post monsoon ant assemblages (Table 7.0-3). Amphibians had a weak but significant relationship with the post monsoon ant assemblage (Table 7.0-3).

Table 7.0-3. RELATE (Primer-e) analysis of Bray-Curtis similarity matrices calculated from square root transformed abundance data with a dummy variable of 1 added. Spearman rank correlation Rho values from 2nd stage MDS analysis of single taxon MDS matrices with each taxon compared to the All Taxa matrix. The null hypothesis was rejected at a significance of P<0.05 with results shown in italics.

Taxon Pairs	**Rho**	**Significance**
Post Monsoon Ants-Ant Combined Surveys	0.175	0.07
Post Monsoon Ants-Amphibians	*0.243*	*0.03*
Post Monsoon Ants-Water Beetles	*0.219*	*0.04*
Post Monsoon Ants-Pre-monsoon Ants	0.012	0.39
Ant Combined Surveys-Amphibians	0.085	0.19
Ant Combined Surveys-Water Beetles	0.1	0.22
Pre-monsoon Ants-Ant Combined Surveys	*0.492*	*0.03*
Pre-monsoon Ants-Amphibians	0.041	0.3
Pre-monsoon Ants-Water Beetles	-0.188	0.94
Amphibians-Water Beetles	*0.264*	*0.02*
All taxa combined-Amphibians	0.353	0.06
All taxa combined-Water Beetles	*0.465*	*0.01*
All taxa combined- Ant Combined Surveys	*0.559*	*0.01*
All taxa combined- Pre-monsoon Ants	*0.44*	*0.03*
All taxa combined- Post Monsoon Ants	*0.483*	*0.01*

7.4 Discussion

There are few studies in the sub-tropics comparing taxa across elevation, latitude, temporal clines and land-use using samples from similar and relatively simple ecosystems. The results indicate very limited cross taxon congruence between the study taxa across 2° latitude and some 1200 m of elevational change and a range of land uses when measured by traditional comparisons of abundance,

species diversity, richness or community evenness. Based on this alone all three focal groups would be rejected as suitable surrogate taxa for the other study taxa, despite their widespread recognition as good representatives (Su et al. 2004; Bilton et al. 2006; Pawar, 2007; Andersen et al. 2015). This supports the need identified elsewhere for alternative metrics (Su et al. 2004; Heino, 2010). Su et al. (2004) suggest one such metric is the comparison of cross taxon congruence in the composition of assemblages.

By comparing community similarity at the macroscale, we report here that spatial distributions of each taxa respond in a predicable way but amphibians and Coleoptera are the most reliable surrogates for environment alone. Spatially dependant environmental factors can be masked by anthropogenic activity as was evidenced in the pre-monsoon ant assemblage which drew together sites with tourism and wind turbine installations (Roque et al. 2017). Wind turbine installation sites are reported to have higher ant species richness than undisturbed sites with different assemblages dominated by disturbance tolerant species (Lutinski et al. 2016). With the MDS data points for both tourism and windfarm sites being close in the pre-monsoon ant ordination we suggest both disturbance forms let in disturbance tolerant species (Fig 7.0-1b). Plateau ant assemblages contain granivorous species with plant associations and trampling resulting from tourism is known to change the plant assemblages perhaps resulting in similar assemblages on widely separated tourist sites in the NWG (Baidya, 2015; Mason et al. 2015; Agarwal, 2017, personal communication).

Assemblages vary over time as well as space as the ecological requirements of the taxa change (Roque et al. 2017). This study found species co-occurrence is temporally variable and can be related to the successional state in the system (Tulloch et al. 2016). NWG plateau plant communities are highly seasonal dominated by ephemeral flush vegetation and resurrection plants which flower and seed at the end of the rains (Porembski & Watve, 2005, Watve, 2013). The number of granivorous ant taxa increases during the dry season changing the assemblage profile (Baidya, 2015). Amphibian

assemblages in the NWG contain explosive breeders that are most easily detected at the start of the rains and may not be present (or easily detectable) later (Gaitonde et al. 2016). Vernal rock pool communities like those in the NWG change during their seasonal life (Garrigues, 1999, Brendonck et al. 2015). Initially their assemblages are dominated by early emergent and colonising species as the pools flood changing to communities of species tolerant of high concentrations of ions and pollutants as the pool dries (Florencio et al. 2016).

Coleoptera were the best surrogates of the other study taxa in the 2nd stage MDS by exceeding the threshold value of $\rho > 0.75$ proposed by Lovell et al. (2007) and wider freshwater biodiversity as they are recognised as excellent surrogates (Bilton et al. 2006). However, they were third in the RELATE analysis after the combined ant and post monsoon ant data sets (Table 7.0-2 & 3). Terrestrial invertebrate species richness can be a surrogate of some aquatic invertebrates and vice versa. If a single survey of a surrogate taxa for assessing spatial similarity or the impact of anthropogenic land use had to be chosen, the results show lentic Coloeptera to be the best representative, if more time is available then additive ant surveys during the dry season are very informative but multi taxa combined provide the most robust result. The results show survey timing may significantly skew results and focal taxon ecology must be considered when designing a surrogate study in these (sub) tropical ecosystems. Should resources permit, using a combination of taxa and surveying through the year provides a more robust indicator of spatial relationships and the impact of land use on plateau assemblages.

7.5 Conclusion

This novel study demonstrates that the common metrics of species richness and diversity are less robust and reflect fewer spatiotemporal changes than assemblage comparisons. A multi-taxa approach and sampling through the seasons produces a much more comprehensive and useful picture of both distribution and the drivers. Anthropogenic land use can significantly influence distribution patterns,

and can be detected by the study taxa, especially when their results are combined. The rocky plateaus in western Maharashtra are highly individual above the escarpment reflecting the heterogenous topography and are significantly impacted by tourism and wind turbine installations. Below the escarpment where there is limited topographical variation plateaus are still separated in most taxa. Low intensity agricultural land use has a smaller impact than other land uses but these plateaus still display differences in all the focal taxa. Knowledge of mutualist relationships within the study taxa will help future study design and careful consideration of temporal assemblage changes is needed to draw valid conclusions. In conclusion for conservation purposes each plateau should be considered a unique ecosystem and consent for land-use changes carefully considered.

Chapter 8. Thesis Discussion

8.1 Study importance and objectives

The study set out to determine if the faunal assemblages on the rocky plateaus in western Maharashtra were the same and if they differed how and at what spatiotemporal scales did structure occur and what drove the pattern? Were the drivers only macroscale climate related to elevation and latitude or did anthropogenic land-use have an impact? Finally, was structuring uniform across all the focal taxa? Not only were the assemblages of the three focal taxa examined but within amphibians the relative importance of individual micro-habitats. Finally, amphibian infection with the fungal pathogen *Batrachochytrium dendrobatidis (Bd)* was studied as a fourth taxa looking for the same potential drivers in both the geographical spread of infection and its intensity.

The landscape forms (lateritic plateaus) studied in the thesis chapters are unique in India. They have recently been recognised as fragile ecosystems at state, central government and now international levels. Yet, very few of them have high level statutory protection. For example Kas Plateau, which is designated a World Heritage Site, lacks the highest level protection. Parts of it, and other plateaus, are almost certainly being degraded by high intensity tourism.

The results in all the research chapters demonstrate not only spatial structuring relating to differences in rainfall and temperature but also the impact of anthropogenic land-uses. As the first study of its type in the NWG the findings are highly important in:

- Devising an informed conservation policy.
- Informing environmental impact assessments of these sites.
- Informing ecological mitigation and restoration. A paper on current post bauxite mine restoration practice has been published by Thorpe &Watve (2016) but does not form a research chapter.

We know from published studies that topographical complexity drives biological variation in many taxa (Ernst and Rödel 2008, Florencio, Díaz-Paniagua et al. 2014). As topographical heterogeneity is greater above the WG escarpment a working hypothesis would predict greater species richness and species replacement (beta diversity) above the escarpment. There may however be confounding factors interfering with the natural distribution. Including island biogeographacical factors and taxon evolutionary history, dispersal ability and anthropogenic disturbance. *Bd* is known to be temperature sensitive (Puschendorf et al. 2011).

The focal taxa were selected with the questions and topography in mind. Amphibians are poor dispersers with high site fidelity, both water beetles and many ants have wings but their dispersal ability is not uniform. All four are known to be impacted by the monsoon. Amphibians, water beetles and *Bd* are positively impacted by rainfall but ants negatively. Seasonal resources are important for all groups. Temperature has a cline along time, elevation and possibly latitude. Rainfall duration and amount varies both with elevation and latitude. Some of the water resources are impacted by anthropogenic land-use which may create pools or alter drainage. Land-use on study sites also removes some resources such as loose rocks and woody plants and may introduce pollutants. This form of disturbance was related to plateau accessibility that was found to be much greater below the escarpment or close to roads.

From the anticipated environmental and habitat heterogeneity it could be expected that plateau differences may occur at a range of scales from within a single or few adjacent plateaus to between large areas for example above and below the escarpment. If individual plateaus are acting as edaphic islands with assemblages including endemics driven by factors limited to individual plateaus then each would need to be carefully considered for protection.

To answer the study questions and to incorporate the range of variables described in the preceding paragraphs taxa assemblage data were collected for each taxon from survey units below plateau scale i.e. individual pool, transect or survey line. Alongside the biotic data fine scale environmental data were collected related to the individual pool, transect or survey line. Plateau disturbance and land-use were recorded as well as elevation, latitude and longitude. Statistical analysis was used to relate biotic

data to the environment at spatial scales but also to disturbance, both land-use type and intensity. Impact of the environment may be seen in different data within a taxonomic group. For example it may skew the species distribution in favour of one functional type over another. To try and detect this data were processed at different levels of organisation:

- Type (species where possible), genera and family were examined separately.
- Alpha diversity of basic units e.g. pool and of plateaus.
- Gamma diversity of the whole survey but as the Regions either side of the escarpment were expected to be different gamma was considered separately for each.
- Species diversity and community evenness.
- Functional groups within the ant data.

8.2 Outline of main findings for individual taxa

The study found individual plateau assemblages of all the focal differed at most spatial scales (Table 7.0-1). Assemblages from above and below the escarpment showed consistent differences in all taxa including *Bd* (Table 7.0-1). Some taxa, in all three main focal groups, were restricted to either the Region below or above the escarpment. For example invasive ant taxa were different in each Region and *Bd* infection was more intense above the escarpment where temperatures are lower but more widespread below it where there are fewer dispersal barriers for amphibians. Species turnover as represented by beta diversity was higher above the escarpment in all three focal taxa. Aquatic taxa were more impacted by environmental changes related to elevation and terrestrial ants by changes related to latitude (Table 7.0-1). Amphibian distribution was driven by macroscale environment and followed some island biogeography expectations. Isolated and undisturbed plateaus had fewer species these were mostly endemic or rare. Closely connected undisturbed plateaus had more species than the isolates sites. The plateaus below the escarpment where connectivity is greater shared more species.

Table 0-1. Taxon assemblage drivers. Tick marks are relative to the importance of each variable. Where that variable only applies to one Region that region is annotated. Annotations: Elev-Plateau Elevation; Inter-Reg-inter-Region; Lat-latitude; E-Z-Eco-zone; LU-land-use; D-I-disturbance intensity; Micro-Hab-microhabitats; Seas-inter-monsoon seasonality; Sur-surrogacy.

Taxa	Elev	Lat	Inter-Reg	E-Z	LU	D-I	Micro-Hab	Seas	Sur
Aquatic Coleoptera	✓✓✓		✓✓✓	✓	✓✓	✓✓	✓		✓✓
Amphibians	✓✓	✓	✓✓✓	✓	HR✓✓	HR✓✓	✓✓✓		
Ants	✓	✓✓	✓✓✓		✓✓✓	✓	✓✓	✓✓	✓✓
Bd	✓✓	✓	✓✓✓		✓	✓			
Combined Taxa	✓✓				✓✓	✓✓	✓✓✓	✓✓	✓✓✓

Water beetle summary

Water beetle distribution was non-random at all levels of organisation and across all spatial scales. Assemblages varied either side of the escarpment and differed significantly with elevation, latitude and land-use, with water temperature and rainfall being important driving factors. Whilst human-induced landscape changes appeared to affect water beetle assemblages this effect was less important than spatial explanatory variables. Intra-plateau assemblages varied with pool type having a substantial effect. Inter-plateau assemblages differed considerably, a finding which has implications for the conservation of these ecosystems, both in the Ghats and elsewhere.

The differences were greatest at the lowest spatial scale i.e. between pools. Alpha and Simpson's Diversity and Pielou's community evenness declined with elevation. Beta diversity increased with latitude, in the whole survey area and above and below the escarpment individually suggesting the impact is driven by changes related to latitude. Anthropogenic disturbance had an impact with pool assemblages most similar at an intermediate level of disturbance. Wind turbine installation had the greatest effect on water beetle assemblages.

Amphibian summary including island biogeography, micro-habitats and Bd *infection*

Amphibian distribution was individualistic at plateau scale with sites above the escarpment more unique than those below. Plateaus above the escarpment contained more Western Ghats endemic amphibian species but had lower species richness. The amount of woody plants, ponds and water conductivity drove anuran distribution with streams, rainfall occurrence during survey, loose rock abundance and pH important to caecilians'. Sites with anthropogenic land-use contained a greater proportion of generalist or disturbance tolerant species most notably on plateaus with tourism or wind turbines. A Bergmann cline was identified in both amphibian families.

Microhabitats were significantly important for 12 of the 21 species found in the survey. Generalist taxa were associated with a greater number of microhabitat types that other taxa. There were statistically non-significant associations for the remaining taxa. Microhabitat distribution was not random but impacted by climate and human activity. Pools and other water bodies were very important for taxa found below the escarpment and woody plants for 44% of those above it. Loose rocks were important for 33% of taxa above the escarpment. Three of the 4 species of caecilian were associated with rocks, soil filled depressions and streams.

The plateaus above the escarpment were islands for amphibians whose distribution. Isolated and undisturbed plateaus (Zenda and Amboli High) had fewer amphibian species these were mostly endemic or rare. In contrast to closely connected undisturbed plateaus (Jagmin) had more species than the isolates sites and these were mostly shared with adjacent disturbed sites (Chalkewadi). The plateaus below the escarpment where connectivity is greater shared more species. Community disassembly appears to be evident with disturbed sites having more widely distributed taxa for example *Hoplobatrachus tigerinus* and *Duttaphrynus melanostictus*.

Bd infection varied between the Regions with a lower intensity wide wider spread below the escarpment. Perhaps this reflects the thermal environment which may be creating a thermal refuge for

low elevation taxa. Of some concern was its detection in endangered and critically endangered species and in two wide spread generalists that have now been found as invasive species in Madagascar.

Ant summary

The greater diversity of niches available above the escarpment, derived from the impact of topographical complexity, is reflected by all the taxa with higher richness in the two-principal ant functional groups, Generalised Myrmicinae and Subordinate Componotini. Ant abundance and richness was lowest just after the monsoon finished. Changes in temperature and rainfall drove macroscale patterns in ant assemblages. Within plateaus land-use was highly important in structuring very seasonal assemblages. All anthropogenic land-use had a negative impact on some functional groups with wind-turbine installation favourable for opportunist species. Floral phenology offers a good explanation of the observed seasonal changes as the assemblage moves towards one more dominated by granivourous taxa as the dry season proceeds and seed resources are likely increasing together with reducing rainfall and increasing temperatures. Woody plants and loose rocks were the most important microhabitats for ants.

Cross taxon surrogacy

Aquatic Coleoptera were the only taxa to exceed the published threshold for surrogates in a 2nd Stage MDS analysis. RELATE, a form of MANTEL test was used to seek support for the MDS result. It varied showing the combined survey ant data set to be a better representative of all the focal taxa but aquatic Coleoptera were second. Amphibians were the poorest canaries in both analyses. Indicating both aquatic Coleoptera and ants are good individual surrogates of wider biodiversity on plateaus but a more robust result is obtained by including multiple taxa in surrogacy based studies.

Combined taxa pattern explanations

Landscape heterogeneity and connectivity are known to be key elements in driving higher diversity in macroinvertebrates (Florencio et al. 2014) and amphibians (Ernst & Rödel 2006, Ernst & Rödel 2008).

Amphibians, and to a lesser extent aquatic Coleoptera, reflected an island biogeography model with isolated undisturbed sites being relatively depauperate. It is more problematic to comment in detail for aquatic Coleoptera as knowledge of their endemicity is poor. Anthropogenic activity appeared to impact both and we suggest the assemblages reported are a result of community disassembly.

Contrary to island biogeography principals the better connected plateaus of the coastal Region had lower water beetle and ant species richness unlike the speciose low elevation amphibians. This may reflect relative thermal tolerances, abilities to manage their thermal environment and dispersal ability. Amphibians are known to have high site fidelity and low dispersal ability. The complex thermal landscape above the escarpment may have a greater impact on amphibians, with their poor dispersal ability, than the other taxa that have some flight ability (Ghalambor et al. 2006). In addition, many High Region plateaus are bounded by rocky escarpments which may be impassable to a non-flying organism, features absent in the coastal area. This environmental complexity has existed for a geologically long time and we propose it as a likely mechanism for the higher endemism rates above the escarpment.

Thermal exclusion from the area below the escarpment and suitable niches above may explain the distribution of *Bd* in the study area. Low elevation temperatures sometimes exceeded *Bd's* upper thermal maxima or were at a level that negatively impacts *Bd's* fitness. The observed impact was the the lower infection intensity in *Bd*. The Low Region may provide thermal refugia from *Bd* but only to taxa that are resident there or can move 500 m downslope. The High Region has a more favourable thermal environment for *Bd* but isolation caused by topographical heterogeneity seems to apply to the

transmission vectors for the pathogen. It is beyond the scope of this thesis to detail the argument for thermal exclusion for any of the taxa affected as it lacks laboratory experimental data for comparison.

The response to the latitudinal cline was patchy suggesting some taxa are more impacted by rainfall seasonality and related pool hydroperiod than others. Water beetle alpha diversity and amphibian beta diversity, species richness and diversity increased with latitude as water beetle beta diversity and abundance declined. It should be remembered that elevation increased with latitude most notably above the escarpment complicating interpretation of the finding.

Combining the three focal taxa found that macroclimate was responsible for large scale patterns in distribution of all groups e.g. regional assemblages above and below the escarpment. Within each Region, seasonal and inter-taxon differences appeared. Overall the low intensity agricultural land uses below the escarpment had less impact on assemblages than tourism and wind turbine installations above. Based on the combined taxa results we conclude that all three groups are good surrogates for macroscale environment with water beetles and ants showing the best cross taxon properties. Ants and water beetles were most sensitive to land use when measured as an assemblage. The traditional comparisons of abundance or species richness were less successful at illuminating spatiotemporal patterns than assemblage comparisons. A finding that supports some previous studies that concluded inter-community assemblage comparisons produced more consistent results than comparisons of species richness (Su et al. 2004, Bilton et al. 2006).

Climate change impacts

Climate change is predicted to fragment the monsoon rains, making them less consistent and predictable. All three focal taxa are likely to be negatively impacted. Water beetles are obligate users of the aquatic environment and whilst they can overcome the extreme disturbance of pool drying by aestivation or migration. Such behaviours are reliant upon their physiological state at the time of

desiccation, too early and the juveniles will probably die. Many plateau amphibians have explosive breeding behaviours triggered by the onset of the rain. A break soon after may lead to eggs and larvae desiccating. Amphibians that breed in micro-pools or have larvae that feed outside of pools are at significant risk of desiccation if a break in the monsoon occurs before they fully metabolise. Many plateau ants start nest building or restoration at the end of the monsoon and a fragmented pattern in rainfall may cause their dry season behaviour to be commenced too early.

8.3 Recommendations for future studies

There are some areas in which the study could be improved or perhaps a better description would be expanded to improve the resolution of the findings:

- It would be both interesting and helpful to investigate seasonal shifts in the amphibian and water beetle assemblages. That information would assist in making comparisons between studies where seasonal changes make data sets incomparable. Ideally to sample through a complete monsoon or year would produce some useful data on when to sample to have the lowest temporal variation.
- Only a limited suite of plateau taxa were sampled, it would be very interesting to know how many of the species found were plateau specialists and therefore rare and threatened? To resolve that question, it would assist in knowing if the same distribution patterns are seen in taxa from more plateaus and the surrounding countryside.
- Cross taxon congruence studies often relate flora to fauna. The data from this study could form the platform for such a comparison and to seek correlation with the impacts of disturbance.
- A novel trapping method was developed for sampling ants that would work on any surface. The survey used single bait which is likely to be selective. It would be interesting to survey the same sites with protein bait and compare the results with our fruit/sugar attractant.

- In all three of the taxon samples are specimens whose taxonomy is not easily resolved. As may be anticipated from isolated highly stressed environments where adaption is a key survival tool novel species may be expected and have already been found in the vertebrates, perhaps it is now the invertebrates turn? Some of the water beetle and ant genera are in urgent need of revision resulting in some the sample being allocated morpho-species identity for analysis.
- Distribution data for ants and water beetles is limited and with much of it old. There has been a great increase in amphibian taxonomy in the Western Ghats in recent years including the northern section. Frequently though, the fieldwork excludes the coastal area, as it is outside the Western Ghats. Therefore, almost all studies from peninsular India have limited elevational focus. As amphibians are highly sensitive to environment related to elevation this seems a missed opportunity and the area either side to the Western Ghats hills should be explored.
- The plateaus contain pools of variable hydro-periods. We observed the more vernal pools tended to lack predators both fish and invertebrate and therefore seem idea predator-prey model systems.

8.4 Implications of the study findings and further research questions

The study results provide the first empirical evidence of the uniqueness of each plateau. In particular this is the first time any attention has been paid to the fauna of the lower elevation plateaus in the coastal area, beyond limited taxonomic investigation. It is also the first quantitative faunal evidence of the damage done by intensive tourism and wind turbine installation, beyond the study on bird collisions with wind turbines (Pande et al. 2013).

- Plateau isolation and individuality is most evident above the escarpment. The coastal plateaus also show individuality along a latitudinal gradient. Our recommendations for action are:

- Any review of conservation policy for the northern Western Ghats should recognise the uniqueness of these habitats and their highly individualistic nature.
- Isolated plateaus with low disturbance should be prioritised for preservation as they are most likely to hold rare species.
- Policy should also recognise the changes in biodiversity induced by anthropogenic land-use on the plateaus which should be monitored and regulated.
- Consideration in development plans should be made to prevent anthropogenic barriers adding to the naturally occurring ones.
- Until the wider distribution and population status of plateau taxa is established they should be accorded high conservation importance, which can if necessary be downgraded later.
- The role of metallic ions in the distribution patterns is poorly understood despite the toxicity of some being widely recognised. It would help refine conservation policy to know where ion levels exceed known tolerances and to identify taxa that are present as they may include adapted taxa.
- *Bd* should be investigated geographically much more widely in India as it appears it may be ubiquitous. Understanding of triggers for the infection to change to lethal Chytridmycosis should urgently be sought?
- Rocky plateaus are threatened ecosystems globally; those in the northern Western Ghats are being damaged and lost at a rapid rate before baseline ecological data is published (Porembski et al. 2016). The data from this study forms such a baseline against which comparisons can be made. It should be helpful in developing restoration policy and site management for many anthropogenic activities including mining.

The monsoon is critical for all the study taxa as it triggers activity as it commences or concludes. Climate change models suggest fragmentation in rainfall patterns which could be catastrophic for some taxa that put all their resources into explosive breeding at the onset of the rains risking the loss of a generation if the rains stop. Coastal populations of water beetles and amphibians may be severely

impacted by temperature increases as they may be close to their upper thermal limit and shifting upslope is problematic with the Western Ghats escarpment creating a 500 m high barrier for many.

Two of the research chapters have already been published the remainder have been, or will shortly be, submitted for publication. Where possible publication has been and will be in open access journals. This information should assist in developing an informed conservation policy to preserve enough of these fragile sites to prevent the extinction of unique species already known to reside on them. It will also help in resolving the Wallacean and Hutchinsonian shortfalls in the northern Western Ghats.

8.5 Overall conclusions

The study plateau focal taxa assemblages suggest each plateau is an individual discrete ecosystems isolated by climate and topography and impacted by anthropogenic land-use changes. They are characterised by unique assemblages containing rare species, many of these unique species that cannot disperse into the matrix or to other plateaus. Plateau individuality is greatest above the escarpment but also exists in the coastal area. Anthropogenic land-use appears to have had a negative impact on plateau biodiversity. It is essential that enough of these rare, fragile and threatened habitats are preserved in order to conserve their unique species.

Appendix 1. For Chapter 2, Aquatic Coleoptera

Table A.1.1. Aquatic Coleoptera classification of the aquatic Coleoptera referred to in the study.

Family	Sub Family	Tribe	Genus	Sub Genus	Species/Type
Gyrinidae	Enhydrinae		Dineutus		cf. indicus
Gyrinidae	Orectochilinae		Orectochilus	Patrus	1
Gyrinidae	Orectochilinae		Orectochilus	Patrus	2
Haliplidae			Haliplus		1
Noteridae	Noterinae	Hydrocanthini	Canthydrus		cf. morsbachi
Noteridae	Noterinae	Hydrocanthini	Canthydrus		2
Noteridae	Noterinae	Noterini	Noterus		1
Dytiscidae	Colymbetinae	Copelatini	Copelatus		
Dytiscidae	Colymbetinae	Cybisterini	Cybister		
Dytiscidae	Colymbetinae	Hydaticini	Hydaticus		
Dytiscidae	Colymbetinae	Colymbetini	Rhantus		
Dytiscidae	Copelatinae		Laconectus		
Dytiscidae	Dytiscinae		Sandracottus		1
Dytiscidae	Hydroporinae	Bidessini	Clypeodytes		1
Dytiscidae	Hydroporinae	Bidessini	Clypeodytes		2
Dytiscidae	Hydroporinae	Bidessini	Hydroglyphus		
Dytiscidae	Hydroporinae	Hydrovatini	Hydrovatus		
Dytiscidae	Hydroporinae	Hydrovatini	Hyphydrus		
Dytiscidae	Hydroporinae	Hyphydrini	Microdytes		cf. belli
Dytiscidae	Hydroporinae	Hyphydrini	Microdytes		cf. sabitae
Dytiscidae	Hydroporinae	Hyphydrini	Microdytes		cf. svensoni
Dytiscidae	Laccophilinae		Laccophilus		chinensis
Dytiscidae	Laccophilinae		Neptosternus		1
Hydrophilidae	Hydrophilinae	Berosini	Allocotocerus		1
Hydrophilidae	Hydrophilinae	Berosini	Berosus		cf. enopleurus
Hydrophilidae	Hydrophilinae	Berosini	Berosus		2
Hydrophilidae	Hydrophilinae	Berosini	Regimbatia		cf. attenuata
Hydrophilidae	Hydrophilinae	Acidocerini	Enochrus		1
Hydrophilidae	Hydrophilinae	Acidocerini	Helochares		1
Hydrophilidae	Hydrophilinae	Hydrophilini	Hydrobiomorpha		cf. rufiventris

Hydrophilidae	Hydrophilinae	Hydrophilini	Hydrobiomorpha	cf. spinicollis
Hydrophilidae	Hydrophilinae	Hydrophilini	Hydrobiomorpha	cf. spinicollis nordica
Hydrophilidae	Hydrophilinae	Hydrophilini	Hydrophilus	1
Hydrophilidae	Hydrophilinae	Hydrophilini	Hydrophilus	2
Hydrophilidae	Hydrophilinae	Hydrophilini	Sternolophus	cf. rufipes
Hydrophilidae	Hydrophilinae	Laccobiini	Laccobius	1
Hydrophilidae	Hydrophilinae	Laccobiini	Oocylus	1
Hydrophilidae	Sphaeridiinae	Coelostommatini	Coleostoma	1

Table A.1.2. Aquatic Coleoptera taxa distribution by the Six Eco-zones.

Taxa	High North	High Central	High South	Low North	Low Central	Low South
Gyrinidae (TOTAL)	**0**	**2**	**0**	**3**	**3**	**7**
Dineutus indicus	0	2	0	3	0	3
Orectochilus Patrus sp.1	0	2	0	0	0	0
Orectochilus Patrus sp.2	0	0	0	0	3	4
Haliplidae	**0**	**0**	**3**	**3**	**0**	**0**
Haliplus sp	0	0	3	0	0	1
Noteridae (TOTAL)	**0**	**4**	**3**	**3**	**6**	**1**
Canthydrus cf. morsbachi	0	3	0	0	0	1
Canthydrus sp.2	0	1	2	0	1	0
Noterini sp.	0	0	1	3	5	0
Dytiscidae (TOTAL)	**322**	**130**	**58**	**23**	**56**	**35**
Clypeodytes sp	110	15	12	1	16	1
Copelatus sp.	71	12	12	9	6	0
Cybister sp.1	0	0	2	1	0	0
Cybister sp.2	2	0	1	0	0	1
Cybister sp.3	0	0	1	0	0	0
Hydaticus sp.	0	1	10	0	0	12
Hydroglyphus sp.	0	0	3	0	0	1
Hydrovatus sp.	0	1	4	1	4	4
Laccophilus chinensis ineficiens	3	3	3	1	23	3
Laccophilus sp.	31	27	2	7	2	6
Lacconectus sp.	30	0	0	1	0	0
Lacconectus sp.1	10	2	0	0	1	1
Microdytes cf. belli	64	1	0	0	0	0
Microdytes cf. sabitae	1	1	4	0	2	0
Microdytes cf. svensoni	4	57	0	0	0	0
Neptosternus sp.	0	3	0	0	0	0
Rhantus sp.	2	0	0	2	0	1
Hydroporinae sp.	3	2	0	0	0	6
Hydroporinae Hyphydrus sp.1	0	1	0	0	2	0
Hydroporinae Hyphydrus sp.2	0	2	0	0	0	0
Hydroporinae Hyphydrus sp.3	0	1	4	0	0	0
Sandracottus sp.	1	1	0	0	0	0
Hydrophilidae (TOTAL)	**44**	**17**	**77**	**9**	**32**	**41**

Allocotocerus sp.	0	0	2	0	0	0
Allocotocerus sp.	0	3	3	3	2	4
Berosus cf. enopleurus	5	0	18	0	0	0
Berosus sp.	15	3	9	0	2	1
Berosus sp.2	1	0	1	0	1	0
Coleostoma sp.	11	4	3	0	1	1
Enochrus sp	0	0	1	0	2	1
Helochares sp.	0	0	11	0	0	5
Hydrobiomorpha spinicolis spp	1	1	7	2	2	12
Hydrophilus sp 1	0	0	4	0	0	0
Hydrophilus sp. 2	0	0	0	0	0	1
Laccobius sp.	10	2	0	1	0	0
Oocyclus sp.	0	3	0	0	0	0
Regimbartia cf. atenuata	0	2	25	3	2	14
Sternolophus cf. rufipes	1	0	3	0	20	2

Table A.1.3. Aquatic Coleoptera. Mean N, mean number of individuals per pool. Alpha (mean N taxa per pool), and Presence/Absence Beta diversity by site with Shannon index (H') and Inverse Simpson index (1-D) listed by site arranged in order of reducing latitude, within High and Low Regions, with Eco-Zone and elevation in m, split into sites above and below the escarpment. Dist. Intensity refers to Disturbance Intensity as described in Table 3; Med.-Medium.

Plateau	Eco-zone	Elevation	Dist. Intensity	Mean N	SE	Alpha	Beta	Simpson Index	Pielou's Evenness
Panchgani	High North	1131	High	6.53	2.91	0.91	22	0.381	0.950
Jagmin	High North	1179	Light	6.73	1.82	1.91	21	0.290	0.701
Chalkewadi	High North	1157	Med.	3.72	0.73	1.7	17.4	0.583	0.841
Mhavashi	High North	1090	Med.	5.33	1.5	1.94	19.125	0.565	0.846
Zenda	High Central	1015	Light	6.47	3.84	2.67	20.231	0.341	0.785
Masai	High Central	974	High	3.22	0.52	2.7	14.959	0.696	0.906
Amboli Low	High South	809	High	1.5	0.79	1.84	16.692	0.855	0.936
Amboli High	High South	854	Light	5.56	1.42	4.14	9.45	0.830	0.939
Shipole	Low North	170	Light	1.28	0.42	1.27	23.533	0.645	0.977
Ratnagiri	Low Central	67	Med.	2.08	0.53	2.06	17.941	0.581	0.944
Lanja	Low Central	156	Light	4.5	1.00	2.34	18.714	0.475	0.904
Kudopi	Low South	90	Light	3.92	1.00	2.35	16.448	0.806	0.947
Dhamapur	Low South	85	Med.	4.07	0.91	1.17	16.448	0.615	0.890

Table A.1.4. Aquatic Coleoptera Multiple Linear Regression output from the DISTLM routine in Primer-e, v7. Margin Vegetation and Base Vegetation are the percentage of the pool margin and base with vegetative cover. DO is dissolved oxygen. Conductivity refers to the ion content of the water measured in µs cm-1. A cut off value of 0.20 was applied to all results. Non-Significant Results are not reported. P<0.05=*, P<0.01=**

Parameter	Prop.	F
All Taxa		
Marginal Test		
Water temperature**	0.028	5.354
Dissolved Oxygen**	0.026	4.894
Marginal Test		
Raining**	0.023	4.331
Gyrinidae		
Marginal Test		
None Significant		
Marginal Test		
Marginal Vegetation	0.022	4.060
Dytiscidae		
Marginal Test		
Dissolved Oxygen**	0.036	7.012
Water Temperature**	0.031	5.787
Marginal Test		
Raining**	0.019	3.638
Hydrophilidae		
Marginal Test		
Water Temperature**	0.026	4.945
Water Conductivity**	0.020	3.782
Marginal Test		
Raining**	0.027	5.025
Turbidity**	0.022	4.053

Table A.1.5. Aquatic Coleoptera Eco-zone and site abundance, mean with standard deviation (SD) shown.

Eco-zone/Region	**Total *N***	**Mean (site)**	**Mean (Region)**	**SD**
High North	376	46.1		39.8
High Central	156	38		34.7
High South	162	21.29		23.7
High			35.1	12.65
Low North	38	8.25		2.9
Low Central	97	20.4		9.69
Low South	86	18.5		11.3
Low			15.7	6.5

Appendix 2. FOR CHAPTER 3, AMPHIBIANS

Table A.2.1. Amphibian taxonomy. Where nomenclature is uncertain the rules of the International Code of Zoological Nomenclature (ICZN) have been followed. Where identification is hampered by cryptic species a most likely identity is shown with the prefix 'cf'.

Order	Family	Sub-family	Genera and Species
Anura	Bufonidae		*Duttaphrynus melanostictus*
Anura	Dicroglossidae		*Euphlyctis* cf. *cyanophlyctis*
Anura	Dicroglossidae		*Fejervarya* cf. *brevipalmata*
Anura	Dicroglossidae		*Fejervarya* cf. *caperata*
Anura	Dicroglossidae		*Fejervarya* cf. *cepfi*
Anura	Dicroglossidae		*Fejervarya* sp.
Gymnophiona	Indotyphlidae		*Gegeneophis* cf. *ramaswamii*
Gymnophiona	Indotyphlidae		*Gegeneophis seshachari*
Anura	Dicroglossidae		*Hoplobatrachus tigerinus*
Anura	Ranixalidae		*Indirana* cf. *chiravesi*
Gymnophiona	Indotyphlidae		*Indotyphlus* cf. *battersbyi*
Gymnophiona	Indotyphlidae		*Indotyphlus maharashtraensis*
Anura	Micorhylidae		*Microhyla ornata*
Anura	Dicroglossidae		*Fejervarya* cf. *sahyadris*
Anura	Rhacophoridae		*Philautus* sp.
Anura	Rhacophoridae	Rhacophorinae	*Polypedates maculatus*
Anura	Rhacophoridae	Rhacophorinae	*Pseudophilautus* sp.
Anura	Rhacophoridae		*Raorchestes* cf. *ghatei*
Anura	Dicroglossidae		*Sphaerotheca dobsonii*
Anura	Micorhylidae		*Uperodon globulosus*
Anura	Bufonidae		*Xanthophryne tigerina*

Table A.2.2. Amphibian species distribution by site and survey timing. Sites without a night entry were not surveyed and should not be considered blank searches.

Site	Species	2013	2014 day	2014 night
Panchgani	*Duttaphrynus melanostictus*	2	1	0
	Fejervarya cf. *brevipalmata*	3	0	0
	Euphlyctis cf. *cyanophlyctis*	0	9	0
	Hoplobatrachus tigerinus	2	3	0
	Raorchestes cf. *ghatei*	4	0	0
Chalkewadi	*Fejervarya* cf. *brevipalmata*	3	4	13
	Duttaphrynus melanostictus	1	0	0
Jagmin	*Euphlyctis* cf. *cyanophlyctis*	0	2	0
	Duttaphrynus melanostictus	0	4	0
	Raorchestes cf. *ghatei*	0	2	0
	Indotyphlus maharashtraensis	2	1	0
Mhavashi	*Fejervarya* cf. *caperata*	0	2	0
	Fejervarya sp.	2	1	0
Masai	*Sphaerotheca dobsonii*	0	1	0
	Hoplobatrachus tigerinus	1	1	0
	Indotyphlus cf. *battersbyi*	3	0	0
Zender	*Indirana* cf. *chiravesi*	3	0	0
	Fejervarya sp.	0	0	1
Amboli Low	*Fejervarya* (*Zakerana*) cf. *caperata*	1	2	1
	Duttaphrynus melanostictus	0	1	0
	Gegeneophis cf. *ramaswamii*	6	0	0
	Xanthophryne tigerina	7	7	13
Amboli High	*Xanthophryne tigerina*	30	42	0
	Hoplobatrachus tigerinus	0	1	0
Shipole	*Fejervarya* sp.	2	0	0
	Microhyla ornata	0	1	0
	Fejervarya cf. *sahyadris*	0	5	0
	Hoplobatrachus tigerinus	7	0	0
	*Philautus*sp.	1	0	0
	*Pseudophilautus*sp.	2	0	0
Ratnagiri	*Hoplobatrachus tigerinus*	5	7	0
	Fejervarya cf. *sahyadris*	0	3	0
	Uperodon globulosus	2	0	0
	Sphaerotheca dobsonii	1	0	0
Lanja	*Fejervarya* cf. *caperata*	1	0	0
	Hoplobatrachus tigerinus	3	1	1
	Gegeneophis seshachari	0	1	0
	Euphlyctis cf. *cyanophlyctis*	0	1	0
	Polypedates maculatus	0	1	0

	Sphaerotheca dobsonii	0	0	1
	Fejervarya cf. *cepfi*	9	2	1
	Fejervarya cf. *sahyadris*	4	1	4
Kudopi	*Gegeneophis seshachari*	8	10	0
	Microhyla ornata	0	1	0
	Hoplobatrachus tigerinus	2	2	0
	Fejervarya cf. *sahyadris*	6	10	0
	Sphaerotheca dobsonii	1	0	0
Dhamabur	*Fejervarya* sp.	10	0	2
	Euphlyctis cyanophlyctis	0	0	1
	Fejervarya cf. *sahyadris*	0	8	5
	Fejervarya cf. *cepfi*	0	0	3
	Sphaerotheca dobsonii	0	0	1
	Polypedates maculatus	0	0	1
	Microhyla ornata	0	0	1
	Hoplobatrachus tigerinus	2	2	0
Total		**136**	**140**	**49**

Table A.2.3. Amphibian species habitat associations and known elevational distribution. IUCN-IUCN Red List Habitat descriptions were used for microhabitat listings except where alternatives are stated: Dt-disturbance tolerant; Ep-ephemeral lentic water; F-forest; Fo-fossorial; Ge-generalist; Gr-grassland; Le-lentic; Lo-lotic; NDt-Not Disturbance Tolerant; Pl-plateau specialist; Ro-loose rocks; S-shrubland; W-wetland. Elev-elevation; IUCN status codes: CR-critically endangered; DD-data deficient; EN-endangered; LC-least concern; NL-not listed. Endemism: NO-not endemic; AS-Endemic to Asia; IN-Endemic to India; WG-Endemic to Western Ghats. End-recorded endemic status; EZ-Eco-zone specimen found in.

Species	**Microhabitats**	**Microhabitat Author**	**Published Elevation**	**Elev**	**IUCN**	**End**
Duttaphrynus melanostictus		IUCN	160-2000	809-1179	LC	NO
Euphlyctis cf. *cyanophlyctis*	Dt, Ep, F, Ge,Le,	Aravind and Gururaja 2012;	160	85-1179	LC	NO
Fejervarya (*Zakerana*) cf. *brevipalmata*	Dt, F, Ge,Gr, W	IUCN	400-1250	1157-1190	DD	WG
Fejervarya (*Zakerana*) cf. *caperata*		Aravind and Gururaja 2012;		156-1090	NL	NO
Fejervarya (*Zakerana*) cf. *rufescens*	Dt, Ep, F, Ge,Lo	IUCN	800	85	LC	WG
Fejervarya sp.				85-1090		
Gegeneophis cf. *ramaswamii*	Dt, F, Fo, Ge,Lo,	IUCN		809	LC	WG
Gegeneophis seshachari	Dt, F, Fo, Pl, Ro	IUCN		90-156	DD	IN
Hoplobatrachus tigerinus	Dt, F, G, Ge,Le, S	Aravind and Gururaja 2012;	160	67-1131	LC	NO
Indirana cf. *beddomii*		IUCN	600-1200	1015	LC	WG
Indotyphlus cf. *battersbyi*	Dt, F, Fo, Ro, S	IUCN		974	DD	WG
Indotyphlus maharashtraensis	Fo, Gr, Ro	IUCN		1179	DD	IN
Microhyla ornata	Dt, G, Ge,S, Le,	Aravind and Gururaja 2012;	281-294	85-170	LC	NO
Minervarya sahyadris	Dt, Ep ,Gr, Le	IUCN		67-170	EN	WG
Philautus sp.				170		
Polypedates maculatus	Dt, F, G, Ge,S,	Aravind and Gururaja 2012;	160	85-170	LC	AS
Pseudophilautus sp.		IUCN		170		
Raorchestes cf. *ghatei*	Pl	IUCN	658-1183	1157-1179	NL	WG
Sphaerotheca dobsonii	Ep, F, Le, S	IUCN	600-1200	67-974	LC	IN
Uperodon globulosus	Dt, Ep, Ge,S, F	IUCN		67	LC	AS
Xanthophryne tigerina	Pl, Ro	IUCN	790-860	809-854	CR	WG

Appendix 3. For Chapter 5, Batrachochytrium dendrobatidis

Table A.3.1. *Batrachochytrium dendrobatidis*. Straight line regression of physiochemical parameters. Temperature = Water Temperature; Elevation is site elevation above sea level.

Variable	**Related to**	**R^2**	**F**	**P**
Temperature	Elevation	0.71	$F_{1,158}$ =384.2	< 0.001
pH	Elevation	0.095	$F_{1,158}$ =16.47	< 0.001
pH	Temperature	0.214	$F_{1,158}$ = 42.75	<0.001

Table A.3.2. *Batrachochytrium dendrobatidis* distribution of mean positive GE values for individuals by geographical region. Standard Deviation-SD.

Region	**Sample n**	**Mean GE**	**SD**	**Minimum**	**Maximum**
All Sites	32	2.0	2.0	0.1	24.3
High Region	14	4.0	7.7	0.1	24.3
Low Region	18	0.4	0.3	0.1	1.1

Appendix 4. For Chapter 6, Ants

Table A.4.1. Illustration of variation in ant assemblages either side of the Western Ghats escarpment, High is above the escarpment and Low below it. The ten most abundant taxa for each land use class with the taxa ranked 1-10 by abundance. F.G. indicates functional group after (Hölldobler & Wilson, 1990; Andersen, 1997; Andersen, 2000; Narendra, 2006; Vineesh, et al. 2007). Only the top ten taxa ranked by abundance are shown. Abbreviations: CCS-Cold Climate Specialist; GM- Generalised Myrmicini; HCS-Hot Climate Specialist; I-Invasive; OP-Opportunist; SC-Subordinate Camponotini; SM-Southern Morph; T-Tramp; TCS-Tropical Climate Specialist.

Type	**F.G.**	**High**	**Low**
Dolichorinae sp 1	DD		7
Formicinae Anoplolepis gracilepes	I & T; OP		4
Formicinae Paratrechina longicornis	I & T; OP	3	1
Formicinae Polyrachis cf *rastelata*	SC	6	
Myrmicinae Aphenogaster beccari	OP		9
Myrmicinae Aphenogaster sp 1	OP	2	
Myrmicinae Aphenogaster sulcaticeps	OP	4	
Myrmicinae Crematogaster artifex	GM		8
Myrmicinae Crematogaster dohrni	GM		6
Myrmicinae Crematogaster hodgesoni	GM	10	2
Myrmicinae Crematogaster rothneyi ssp1	GM		5
Myrmicinae Crematogaster rothneyi ssp2	GM	5	
Myrmicinae Monomorium aberrans	HCS	8	
Myrmicinae Monomorium indicum	HCS		10
Myrmicinae Monomorium indicum ssp	HCS	1	
Myrmicinae Monomorium mayri	HCS	7	
Myrmicinae Myrmica smythesii	OP	9	3

Table A.4.2. The ten most abundant ant taxa for each land use class, ranked 1-10 by abundance. High is above the escarpment and Low below. F.G. indicates functional group after (Hölldobler & Wilson, 1990; Andersen, 1997; Andersen, 2000; Narendra, 2006; Vineesh, et al. 2007). Light = sites with low disturbance; Tour = Tourism; Wind = Wind Turbine installations; Agri = Agriculture. Abbreviations: CCS-Cold Climate Specialist; GM- Generalised Myrmicini; HCS-Hot Climate Specialist; I-Invasive; OP-Opportunist; SC-Subordinate Camponotini; SM-Southern Morph; T-Tramp; TCS-Tropical Climate Specialist.

		High Region			Low Region	
Type	**F.G.**	**Light**	**Tour**	**Wind**	**Light**	**Agri**
Dolichorinae Iridomyrmex type	DD				5	
Formicinae Anoplolepis gracilepes	I & T; OP					5
Formicinae Camponotus sericeus, SM	SC	9		9	4	
Formicinae Lepisiota sericea	SC	6		8		
Formicinae Oecophyla smaragdina	TCS					10
Formicinae Paratrechina longicornis	I & T; OP	2		2	1	1
Formicinae Polyrachis cf rastelata	SC		3			
Formicinae Polyrachis exercita	SC		8			
Formicinae Polyrachis hauxwelli	SC		10			
Formicinae Prenolipsis sp 1	CCS			5		
Formicinae Psuedolasius sp	TCS	5				
Myrmicinae Aphenogaster beccari	OP	8				4
Myrmicinae Aphenogaster sp 1	OP		2	10		
Myrmicinae Aphenogaster sulcaticeps	OP			1		
Myrmicinae Crematogaster artifex	GM				6	6
Myrmicinae Crematogaster dohrni	GM				3	
Myrmicinae Crematogaster hodgesoni	GM		5		2	
Myrmicinae Crematogaster rothneyi ssp*1*	GM	1			8	
Myrmicinae Crematogaster rothneyi ssp2	GM				7	3
Myrmicinae Monomorium aberrans	HCS	4	9			
Myrmicinae Monomorium indicum	HCS		6			10
Myrmicinae Monomorium indicum ssp	HCS		1		10	
Myrmicinae Monomorium mayri	HCS	3		6		
Myrmicinae Monomorium pharaonis	HCS			7		
Myrmicinae Monomorium sp	HCS			3		
Myrmicinae Monomorium subopactum	HCS			4		
Myrmicinae Myrmica smythesii	OP		4			2
Myrmicinae Myrmica sp	OP		7			
Myrmicinae Pheidole sharpi	GM	7				
Myrmicinae Phiedole sp	GM					7
Myrmicinae Tetramorium guineese	OP	10				
Myrmicinae Tetramorium sp 2	OP					9
Myrmicinae Volenhovia sp	TCS					8

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